polypides, and the restriction of the polypides and their buds to separate tubes. I propose for it the name *Cephalodiscus nigrescens*.

EXPLANATION OF PLATE.

Photograph of the Natural Size of a Specimen of *Cephalodiscus nigrescens*, Lankester, from the Antarctic Ocean.

Experimental Researches in Vegetable Assimilation and Respiration. IV.—A Quantitative Study of Carbon-Dioxide Assimilation and Leaf-Temperature in Natural Illumination.

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CONTENTS.

Section I.—*Introduction. Apparatus and Procedure.*

It has been made evident by the experiments recently published by one of us,* that the amount of carbon-dioxide assimilation which a leaf is actually performing, or is capable of performing, is profoundly affected by the temperature of the assimilating cells.

Neglect of this factor has been a fruitful source of confusion in attempts to estimate the effect of different intensities of light upon the process of assimilation.

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* "Experimental Researches on Vegetable Assimilation and Respiration. III.—On the Effect of Temperature on Carbon-dioxide Assimilation," by G. L. C. Matthaei, 'Phil. Trans.,' B, vol. 197, 1904; to be referred to as "Assim. and Resp. III."

Particularly is this the case when *natural* illumination is being investigated, for the diffuse light of the sky produces but little heating effect, while direct solar radiation may heat up a leaf considerably.

During the summer of 1904 we have been working at the relation between carbon-dioxide assimilation and the intensity of natural illumination. For this work we determined the real internal temperatures of our assimilating leaves by the thermo-electrical method described in "Assim. and Resp. III," p. 76. Without the exact data as to the relation between temperature and assimilation set out in that paper, and without the knowledge gained when working with artificial light, we should have been quite baffled in our attempt to deal in detail with all variations of natural light.

In several directions the present paper is of a "preliminary" nature, and we hope to complete the work next summer.

We determined, at the outset, to work in the open air, so as to be able to use direct sunlight, and to avoid the use of heliostats and reflecting silver surfaces.*

The general experimental and analytical procedure has been the same as in "Assim. and Resp. III."

As it was, however, impossible to work sensitive aspirators and a galvano-meter satisfactorily when they were exposed to direct or intermittent sunshine, these parts of the apparatus were set up in a north room of the laboratory. Thence they were connected by 50 feet of tubing and wires to the leaf chamber, and to the baryta-absorption-tubes situated on a table on the flat roof of the new University Botany School. On this spot sunshine, when vouchsafed, is continuously available, without any interfering shadows, for quite 12 hours daily, in the height of summer.

In addition, gas for heating, and running water for cooling are there conveniently to hand, so that the temperature of the leaf in its chamber can be fully controlled. Without all these facilities, such as are afforded by very few botanical laboratories, our particular work would have been impossible.

The leaves employed were those of cherry-laurel and of *Helianthus tuberosus.* With the former we have worked for some years, and the latter were employed in order to test whether such a different type of leaf would give similar results.

The cut leaf is set up in the usual flat leaf-chamber with a fixed glass front and an adjustable glass back, through which pass the wires from the thermo-junction in the leaf to the galvanometer.

* Langley ('Phil. Mag.,' 1889, p. 10) has shown that the various solar rays are reflected in slightly different proportions by polished silver, and also that the least tarnishing is a serious disturbing factor.

The chamber is submerged in a fixed position on a wooden frame in a large rectangular glass cell full of water (a polished museum-jar measuring 12 in. × 7·5 in. × 3·5 in.); see fig. 1.
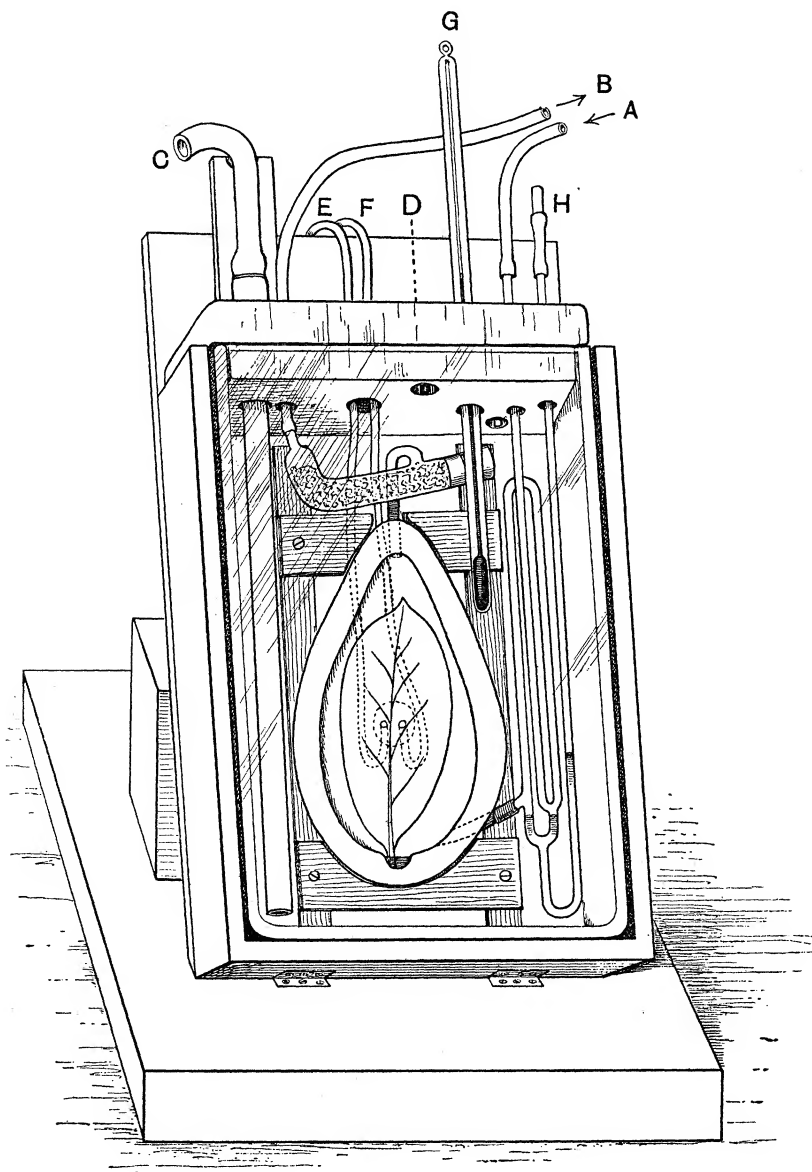

FIG. 1.

This water-bath is closed above by an oblong thick cork cut to fit the mouth.   Through appropriate holes in the cork pass:—the air-current

tubes, from the CO_2-generator to the chamber (A), and from the chamber to the Pettenkofer tubes (B); the fine rubber tubes (E) and (F) to the back of the chamber, containing the electric wires; an inlet tube (C) from the water supply, passing to the bottom of the bath, and wide enough to carry a rapid circulation of water; holes (D) for the outflow of the water, which was allowed to stream down the back of the bath; and (G) a thermometer, to indicate the bath-temperature. The air-current which enters at (A) passes through a thrice bent glass tube, to give it time to acquire the bath-temperature. The end (H) of this system of glass tubes can be opened when required to let water into it, and this water gravitates at once into the chamber to keep up the supply for the leaf.

The air-current leaving the leaf-chamber by the tube at its apex, passes through a tube of calcium chloride to be dried; condensation in the cooler tube outside the bath is thus prevented.

The water-bath fits into a wooden support resembling an upright box without front or top, painted black inside, and hinged by its lowest edge to a substantial base-board. This hinge permits movement in a vertical plane ranging from the horizontal to the vertical positions. The base-board can be rotated horizontally on a central pivot fixed on the table. By these two movements the bath with the contained leaf-chamber can be adjusted by hand so as to be kept at right-angles to the incident sun's rays throughout an experiment.

The necessity for tilting the bath to follow the vertical displacement of the sun made it difficult to heat from beneath with a burner; the heating was therefore achieved by carrying the water-current, before it reached the bath, through a laboratory water-heater of the horizontal flanged-tube pattern. By varying the amount of gas burning and the rate of the water-flow any temperature above the summer temperature of the running water could be obtained in the bath.

The water-heater was carefully boxed in so as to be protected from the wind, and a subsidiary thermometer was placed in the water-current close to the exit from the heater. This did away with the risk of excessive alterations of temperature, as it gave immediate notification of the full effect of any readjustment of the heating long before the large mass of water in the bath, and the bath-thermometer, reached the corresponding temperature.

As the leaf in its chamber was only two inches from the front of the bath, it received, when exposed freely, the diffuse light from more than a third of the hemisphere of the sky, which at this level, on the roof, is very little interrupted by the tops of adjacent trees.

When it was desired to expose the leaf to the sunlight alone without the

general diffuse light, a wooden tube of somewhat bigger section than the leaf, and about four feet long, was fitted tightly on to the front of the bath so as to cut out practically all the diffuse light. An oblique observation-hole cut near the base of the tube allowed the illumination of the leaf to be inspected. For exposure to diffuse light alone, while the sun was shining, a thin board, about 18 inches square, fixed obliquely at the end of a 20-foot batten, was supported high up in the air so as to cast a shadow on the leaf. This hindered the access of only a small portion of the diffuse sky light, but had, of course, to be carefully watched and shifted by hand that a shadow might always be kept on the leaf.

For certain critical experiments it became essential to have known fractions of the sun's luminous radiation falling upon the leaf. An account of the method adopted to ensure this will be found in Section V.

Section II.—*On the Internal Temperature of Leaves Exposed to Natural Illumination.*

In a previous paper[*] we have shown that the radiation from a high-pressure incandescent gas-light of nominal 1000 candle-power, causes a considerable rise in the internal temperature of leaves exposed close to it even after the radiation has passed through a thick stratum of water.

It becomes, therefore, important to determine what heating effect natural illumination, and, in particular, full normal insolation will produce.

The greater part of the dark-heat radiation from a source of light would be absorbed by interposed water and glass, but a further amount of radiation, not utilisable for the chemical work of assimilation, is absorbed by the more opaque leaf and some excess temperature of the leaf over its environment is inevitable with powerful light.[†]

With leaves exposed to bright light in a slow current of damp air there is not very much cooling of the leaf by evaporation and the internal leaf temperature is a factor that cannot be ignored.

In the present section we shall consider, in some detail, a few cases which illustrate the temperatures that can be attained inside leaves exposed to various degrees of natural illumination, on the one hand when the leaf is in the open air, and on the other hand when it is enclosed in a glass chamber, with or without water-cooling. The temperatures are in all cases determined thermo-electrically.[‡]

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[*] " Assim. and Resp. III," p. 75.

[†] A crystalline transparent alum-plate would cut off somewhat more heat, but this is an impracticable expedient, while alum solution is rather less efficient than water, *cf.* Shelford Bidwell, 'Brit. Assoc. Reports,' 1886, p. 309.

[‡] For details of procedure, see " Assim. and Resp. III," p. 76.

We will take first two special experiments with leaves of cherry-laurel in the open air, and subsequently one in which the leaf is in a glass chamber, sunk in a water-bath (the normal arrangement in our assimilation experiments).

For the experiments in the open air, the cut leaf was pinned out by its margin on a small thin rectangular board which was hinged by its lower edge to a large rigid horizontal base-board. Through the thin hinged board was an oval opening, only a little smaller than the leaf, and over this the leaf was stretched.

The stalk of the leaf dipped into a little well of water in the base-board and remained in the water at whatever angle the hinged frame might be sloped. A thermo-junction was inserted in the mid-rib of the leaf and the free ends of the wires hung down into mercury-cups on either side of the water-well. Supported in a hole through the base-board was a funnel which contained a thermometer and the control thermo-junction, and could be filled with water at any desired temperature. The whole of this part was carefully screened from solar or indirect radiation. The two junctions were connected up with one another and with the galvanometer by wires running to mercury-cups in the horizontal board.

On July 17, 1904, the sun shone with unclouded brilliance throughout the day. A leaf was set up on the hinged frame and the following temperature observations were made by means of the galvanometer.

Hour.	Conditions.	Leaf-temperature.
A.M.		° C.
11.25	Leaf in shade ; shade-temp., 27° C.	28·0
11.50	Leaf vertical, facing south in direct sun. Bright	38·3
11.53	mercury thermometer in sun, 30°·5 C.	39·8
11.55		39·3
P.M.		
12.7	Frame inclined till leaf is normal to the solar radiation	44·6
12.10	A glass plate interposed in front of leaf..............	44·3
12.20	Glass plates also behind, above, and at sides, within an inch of leaf, boxing it in	51·0
12.25	Visible brown spot of killed cells.	
12.28	Sun-temp., 32° C. Front and top glasses off, others remaining	44·5
12.35	All glass plates taken away............................	41·4
12.38	Leaf-frame placed vertically	39·0
12.45	Large rectangular cell of water (temp., 23° C.) close to leaf in front, leaf closed in behind, above, and at sides with glass plates	41·8
	Experiment ended as leaf is extensively turning brown, killed by the heating to 51° C.	

Hour.	Conditions.	Leaf-temperature.
P.M.		° C.
2.30	A new leaf set up. Leaf in shade.	
2.40		28·1
2.45	Temp. in shade of chimney, 27°·3 C. (Sun-temp.,	28·1
2.50	32° C.)	28·6
3.0		28·6
3.10	Sun's radiation reflected on to the leaf from plane glass mirror	33·0
3.17	Ditto, but water-cell in path of reflected rays	30·4
3.20		29·6
3.22	Mirror removed	28·4
3.23	Water-cell removed	28·2
3.24	Mirror replaced without water-cell...................	30·1
3.27	Substituted a mirror of thin glass	31·0
3.30	Mirror removed..	28·0
3.34	Leaf moved into direct sunshine, leaf vertical	31·7
3.36		33·6
3.39	Leaf at right angles to solar radiation. Sun-temp., 29°·4 C. ; shade-temp., 26°·7 C.	33·6
3.47	A cell full of water (25° C.), 1 inch in front of leaf	31·3
3.50	All shaded with black cloth	26·6
4.0	Leaf moved into shade, boxed in with glass plates.	28·4
4.4	Shade-temp., 26°·3 C.	28·5
4.6	Sun reflected by mirror on to boxed-in leaf in shade	36·5
4.10	Back glass alone removed. Shade-temp., 25°·3 C.	30·7
4.20		29·9
4.27	Leaf vertical in direct sun with front glass on alone	33·2
4.33	Leaf boxed in by adding the other glass plates...... Experiment stopped. Shade-temp., 25°·2 C.	42·6

We may sum up these observations as follows :—

Experiments in Direct Sunshine.

Excess of Internal Temperature of Leaf in Brilliant Sunshine over Reading of adjacent Bright Mercury Thermometer in the Sun.

Hour.	Conditions.	Excess leaf-temperature.
		° C.
Noon	Leaf vertical	8—7
„	Leaf normal to sun's rays	13—9
„	Leaf normal in glass chamber.....................	20
„	Ditto, behind water-cell	10
About 4 P.M. ...	Leaf vertical	2—5
„ ...	Leaf normal to sun	4
„ ...	Ditto, behind water-cell	2
„ ...	Leaf normal to sun, in glass chamber...........	14

Experiments in Shade.

Excess of Internal Leaf-Temperature in Shade, on Cloudless Day, over adjacent Thermometer Reading.

Hour.	Conditions.	Excess leaf-temperature.
		° C.
Noon	Leaf in open air	1
3.30 P.M.	,, ,, ...	1—1½
,, ...	Reflected sun on leaf	6
,, ...	Reflected sun through water	3
,, ...	Leaf in glass chamber	2
,, ...	Ditto, reflected sun on chamber	10

The raising of the leaf-temperature in a leaf surrounded with glass plates when lighted by direct or reflected sunshine is very striking, and we see why observers have always failed with attempted estimations of assimilation in bright direct sunshine when the procedure has been simply to place the leaf in an unprotected glass tube in the sun.

With adequate water-cooling the tube could be exposed to the sun without killing the leaf, but even then the temperature of the leaf would be very much raised.

This heating up of the leaf will, no doubt, partly be due to checking of transpiration in the enclosed space, but the effect comes on so quickly that it must chiefly be due to "the greenhouse effect," the imprisonment of the reflected dark-heat rays by the glass plates which are almost impervious to them.

We may now give some details about the internal temperature of a cherry-laurel leaf placed, as in our assimilation experiments, in the flat glass "leaf-chamber," and this sunk in a large glass bath of running water, *cf.* fig. 1.

The chamber was adjusted at right angles to the sun's radiation and the leaf-temperature was determined at the galvanometer at intervals of exactly one minute. At the same moment the state of the natural illumination was written down by an independent observer. The observations were made on July 20, 1904. Clouds were drifting irregularly across the sun and the determinations start at 12.4 P.M., just as a large cloud cleared away from the sun. It may be stated at once that there is a lag of about one minute between the change of insolation and the temperature-change that results, so that in the table the temperature at the subsequent minute really corresponds to each particular illumination :—

Temperature of water-bath.	Time.	Illumination.	Leaf-temperature.
			° C.
Bath-temp., 18°·6 C.,	12.4	Brilliant sun	22·4
water circulating	.5	Moderate sun	27·3
quickly	.6	Brilliant sun	27·8
	.7	Moderate sun	29·0
	.8	Bright sun......................	26·7
	.9	Brilliant sun	24·6
	.10	Very brilliant sun..............	28·3
	.11	Thin cloud......................	29·0
	.12	Thick cloud	24·9
	.13	Thicker cloud	23·4
	.14	Sun quite obscured	22·3
	.15	Thick cloud	21·8
	.16	Thin cloud	22·7
	.17	Sun quite obscured	21·9
	.18	Thick cloud	22·2
Bath-temp., 18°·4 C.	.19	Sun quite obscured	21·9
	.20	Sun gleam.......................	24·3
	.21	Thick cloud	22·5
	.22	Thin cloud......................	22·5
	.33	„	23·9
	.34	Moderate sun	24·3
	·35	Bright sun.......................	25·4
Bath-temp., 18°·8 C.	.35½	Surface darkened with cloth	
	.36	Dark superficially..............	24·7
	.37	„ „	20·2
	.38	„ „	19·4
	.39	„ „	19·4
	.40	„ „	19·3
Bath-temp., 18°·8 C.	.40½	Cloth removed.	
	.41	Brilliant sun	22·3
	.42	Bright sun......................	27·7
	.43	Brilliant sun	27·9
	.44	„	30·0
	.45	„	30·7
Bath-temp., 19°·3 C.	.46	„	29·7

These readings show how decidedly the temperature of a leaf under experi-mental conditions is affected by variations in the intensity of solar radiation : while the bath (through which, of course, water is running rapidly) only varied in temperature 1° within the 40 minutes, the leaf-temperature oscillated up and down with the varying fine shades of natural illumination through a range of 9°.

If the natural light is variable, very frequent galvanometric readings must be taken to arrive at a real average temperature for a given assimilation-

reading. When a knowledge of this is important, and the light is variable, we have taken the temperature as often as every 3 minutes, all through the experiment.

The difference between the observed temperature of the water-bath and the determined temperature of the leaf gives a rough practical measure of the intensity of the radiation falling on the leaf, and in some experiments this has been calculated for each reading, and used to elucidate the contemporaneous assimilation-values.

If the temperature of the bath and also that of the leaf be plotted graphically, as in figs. 4 and 5, we get in their difference a continuous record of the approximate light intensity.

During all the later experiments, records of the air shade-temperatures and of the readings of a black-bulb-in-vacuum thermometer in the sun have been kept, but we have not thought it important to publish these.

A single extract (Experiment VI, July 24, 1904) may be given here to show the relation of the whole set of temperatures.

Time.	Illumination.	Shade-temperature.	Bright mercury thermometer in sun.	Vacuum thermometer in sun.	Bath-temperature.	Leaf-temperature.
A.M.		° C.	° C.	° C.	° C.	° C.
11.23	Dull	23 ·9	24 ·5	36 ·5	19 ·7	24 ·3
11.30	Gleams of sun	24 ·1	24 ·8	37 ·5	19 ·7	22 ·4
11.44	Fair sun	24 ·8	25 ·5	42 ·0	20 ·2	26 ·9
11.53	Brilliant sun............	25 ·8	28 ·0	54 ·5	20 ·6	27 ·0
P.M.						
12.2	Dull	24 ·7	24 ·6	39 ·0	19 ·7	21 ·5
12.20	Steady dull	24 ·0	25 ·1	37 ·5	19 ·8	21 ·5
1.10	,, ...	23 ·8	24 ·0	29 ·5	19 ·3	21 ·5
1.20	Clearing	24 ·5	24 ·7	36 ·0	19 ·7	21 ·9
1.31	Sun coming out	25 ·4	26 ·4	41 ·0	20 ·0	25 ·4
1.42	Bright sun	26 ·1	27 ·4	48 ·5	20 ·6	28 ·4
1.51	Sun and thin cloud ...	25 ·7	26 ·7	50 ·0	20 ·8	27 ·4

However obscured the sun may be, it is always found that the diffuse light of the sky, according to its brightness, heats up the leaf 1°, 2°, or even 3° above the temperature of the bath.* This demonstrates the greater effectiveness, in absorption of radiation, of the coloured and semi-opaque leaf over the colourless and transparent glass and water.

Such high temperatures in ordinary leaves in the sun are somewhat

* It is only after darkening the water-bath with a black cloth that the temperature of the leaf falls as low as that of the bath.

unexpected.[*] For succulents, and for them only, have such temperatures been previously demonstrated.[†]

Besides a profound influence on respiration, and hence on assimilation, this internal heating up of leaves in bright light may have an important and hitherto unrecognised bearing on quite other phenomena, such as the success or failure of inoculation of leaves by the germ-tubes of parasitic fungi, etc.

Section III.—*Assimilation in Natural Illumination.*

We now pass to a consideration of the relation of leaf-temperature and intensity of illumination to the observed values of assimilation under various natural conditions.

A brief account of the relation of CO_2-assimilation to temperature must be given first.

In "Assim. and Resp. III" there have been given full data, and also the first principles of this relation. A further theoretical consideration of these principles will be found in a contemporary article by one of us.[‡] We may here sum up as much as will concern us.

1. For each temperature at which the assimilating cells of a leaf may find themselves, there is a particular maximal amount of assimilation possible. No increase in the amount of incident light or of available CO_2 will cause the leaf to assimilate more if the temperature remains unchanged. If there is not enough CO_2, or not sufficient light available, then one of these becomes a "limiting factor," and the maximal assimilation for the temperature cannot be attained, but some smaller amount only.

2. The temperature-maxima for assimilation increase rapidly as one ascends the temperature scale, the relation between temperature and assimilation being very similar to the relation between temperature and respiration.

3. At moderate temperatures a leaf can maintain its assimilation at the maximal value continuously for a considerable time, but at higher temperatures (towards 30° C. for cherry-laurel) the initial maximal value is not maintained; instead, a regular falling-off sets in.

4. This decline from the initial value is, for each temperature, more rapid at first than subsequently. The higher the temperature the more precipitous is the whole declining curve. These phenomena necessitate the introduction of a "time-factor" into assimilation values at high temperatures.

The added complication of a time-factor makes critical work with varying

light and other varying factors very difficult at really high temperatures. These relations will form the subject of a separate communication.

In the present work the temperature of the leaf rarely exceeds 30° C., and the duration of the individual experiments is usually not long, so that not much correction need be made for the time-factor. It will be mentioned when this becomes necessary.

It will be convenient to state for future reference what amounts of assimilation we shall take as maximal for the different temperatures concerned in this work.

The data for cherry-laurel are to be found in "Assim. and Resp. III." The final curve, given in fig. 6 of that paper, was smoothed out by free-hand to the curve C in fig. 2 of this paper. The data used for it represent the assimilation-values two hours after the initial moment of heating to the required temperature. The *initial* values will, at high temperatures, be greater, and their precise value depends partly on a hypothesis discussed elsewhere.* These initial values are represented by the curve B, which below 25° C. coincides with the other curve, C.

The values for each degree of the curve C are set out below, being expressed in grammes CO_2, assimilated per 50 sq. cm. per hour.

°C.		°C.		°C.		°C.	
9	0·0038	16	0·0065	23	0·0103	30	0·0151
10	0·0041	17	0·0070	24	0·0109	31	0·0160
11	0·0045	18	0·0075	25	0·0115	32	0·0171
12	0·0049	19	0·0080	26	0·0121	33	0·0182
13	0·0053	20	0·0085	27	0·0128	34	0·0193
14	0·0057	21	0·0091	28	0·0135	35	0·0205
15	0·0061	22	0·0097	29	0·0143		

The curve A represents the curve of initial assimilation-maxima for *Helianthus*. It is based on such observations in the present paper as are undoubtedly maximal. Four of these are above all suspicion, as follows:—

		°C.
Experiment X	0·0090 at	18·0
„ XI.	0·0109 at	20·7
„ XI.	0·0131 at	22·3
„ XVI	0·0290 at	30·0

The values for the two leaves are fairly close together at 18° C., but at 30°·0 C. *Helianthus* has gone up out of proportion to cherry-laurel, *i.e.*, it has a larger coefficient of temperature-acceleration.

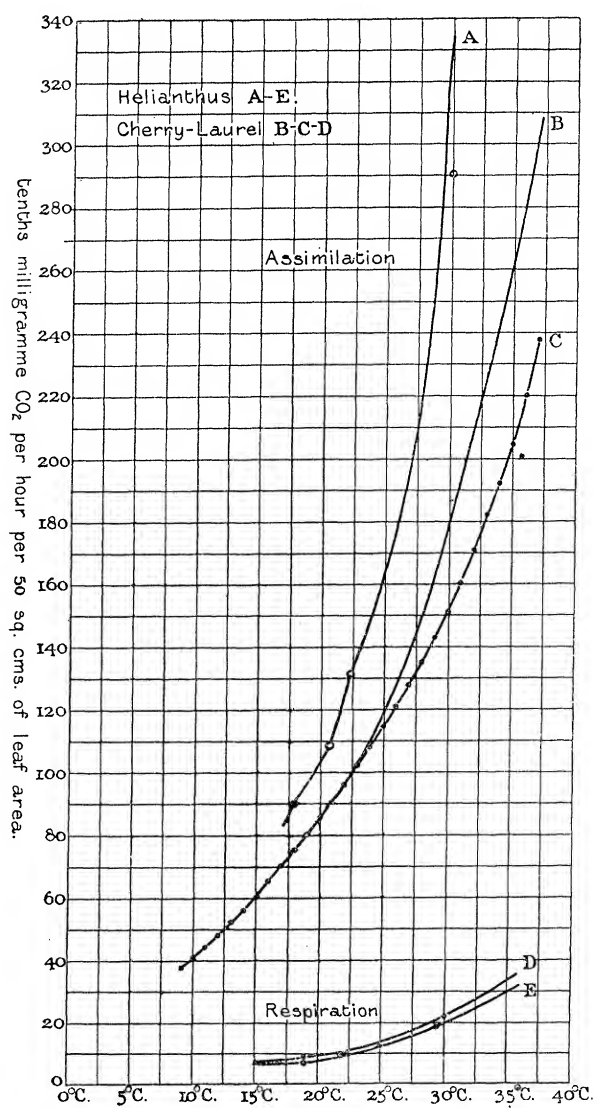* F. F. Blackman, "Optima and Limiting Factors," *loc. cit.*

Fig. 2.

The curves D and E represent the respiration of the two leaves, cherry-laurel and *Helianthus* respectively, at the various temperatures, expressed in grammes CO_2 per 50 sq. cm. leaf-area per hour. The values determined were as follows:—

Helianthus......... Experiment IX, 0·0018 at 29°·5 C.; Experiment XVI, 0·0007 at 19°·0 C.

Cherry-laurel...... Experiment XIII, 0·0021 at 30° C.; Experiment II, 0·0009 at 19°·0 C.; and Experiment III, 0·0008 at 18°·4 C.

In the experiments in "Assim. and Resp. III," it was demonstrated for cherry-laurel that the assimilation-maxima at a given temperature were practically identical for all similarly treated leaves of the same age on the same evergreen bush at any one season of the year. In July and August, 1904, when our new experiments were performed, the cherry-laurel bears new leaves just come to maturity and also leaves of the previous year. Experiment showed that the latter have by now quite low assimilation temperature-maxima, but that the newly matured leaves give the same values as we found in April, 1902, and April, 1903. This agreement for three separate years gives one considerable confidence in this material.

Occasionally a leaf will show marked individuality and give aberrant values, but this is very rare; Experiment XII furnishes a case.

Let us consider firstly some preliminary experiments with various natural variations of illumination.

As the object of this work has been to determine completely the relations between assimilation and all intensities of natural illumination, and, as our previous work has shown that it would be fallacious simply to regard a succession of assimilation readings in a succession of different illuminations as being solely determined by the light, it therefore becomes essential to make inquiry about each assimilation-value obtained, and to determine (either experimentally or statistically) whether the assimilation is or is not being limited by the temperature of the leaf to a smaller amount than the light would provide. In the early experiments this point is not examined experimentally, but is argued out by reference to the data on p. 413, and sometimes to data obtained in subsequent experiments.

In the first four of these experiments on illumination, the actual leaf-temperature was not determined thermo-electrically, but has been subsequently roughly estimated by adding to the temperature of the bath such allowance as later exact experiments showed to be appropriate for each condition of illumination.

Experiment I.—Cherry-laurel; leaf of current year set up in the leaf-chamber during the night in bath with moderate flow of water through it, and no artificial heating throughout the experiment. The bath at first vertical and superficially darkened with black cloth. From 4.15 to 5.15 A.M., an estimation of the darkened leaf was taken, which shows an apparent minute absorption of CO_2. This is probably somewhat in error, as a slight respiratory production of CO_2 would have been expected; the chamber was, however, not perfectly dark. As soon as the rising sun shone on the bath— at 6 o'clock—the black cloth was removed, and the bath adjusted by means

Experiment I (July 12, 1904).—Cherry-laurel ; Weight, 1·60 grammes ; Area, 50·3 sq. cm. ; Current Rate, 810 c.c. ; CO_2 = 2·3 per cent. (average).

Exposure.	Time.	Illumination.	Temperature of bath.	Estimated temperature of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
Leaf-chamber darkened with cloth	A.M. 3.15—4.15	Bright dawn, sunrise 3.58	15·5		Preliminary		
	4.15—5.15		15·8 16·1	16·0	0·0346	0·0001	[0·0008]
6 A.M., leaf-chamber lighted ; thenceforward adjusted continuously normal to sun, *plus* diffuse light	5.15—6.15 6.0	Sun on chamber...	16·6	16·6	0·0366	0 0014	transition
	6.15—7.15 7·0	,, no clouds ... ,, ,, ...	18·2 20·1	21·1	0·0370	0·0082	0·0092
	7.15—8.15 7.45	,, ,, ... ,, light clouds....	21·7 20·5	25·4	0·0390	0·0104	0·0117
	8.15—9.15 8.50	,, ,, ... ,, cloudless	23·5 24·5	26·7	0·0400	0·0110	0·0126

All amounts of CO_2 are expressed in grammes. The values in the Real Assimilation column are in this and all subsequent cases arrived at as follows :—The value for CO_2 absorbed by the leaf (in previous column) is brought to the value per hour and then reduced to an area of 50 sq. cm. To this is added the respiration value per hour (from the curves D or E in fig. 2) corresponding to the measured or estimated temperature of the leaf. Fifty sq. cm. was chosen as the standard area because it approximates very nearly to the actual sizes of the leaves. When a single temperature only is given for an estimation it may be taken that it is the mean of a number of observations ; in a few cases it has been thought worth while to give the details.

of its horizontal and vertical movements until the leaf was normal to the sun's rays. After a quarter of an hour "preliminary" an estimation of the combined effect of low direct sun and diffuse light was made—6.15 to 7.15 A.M. During this and subsequent readings the chamber was readjusted to face the sun every 10 minutes.

Throughout the series of readings the temperature of the bath rose continually, as the sun, shining on the supply-water-pipe and on the bath, gained in power; the rate of water-flow remained unaltered.

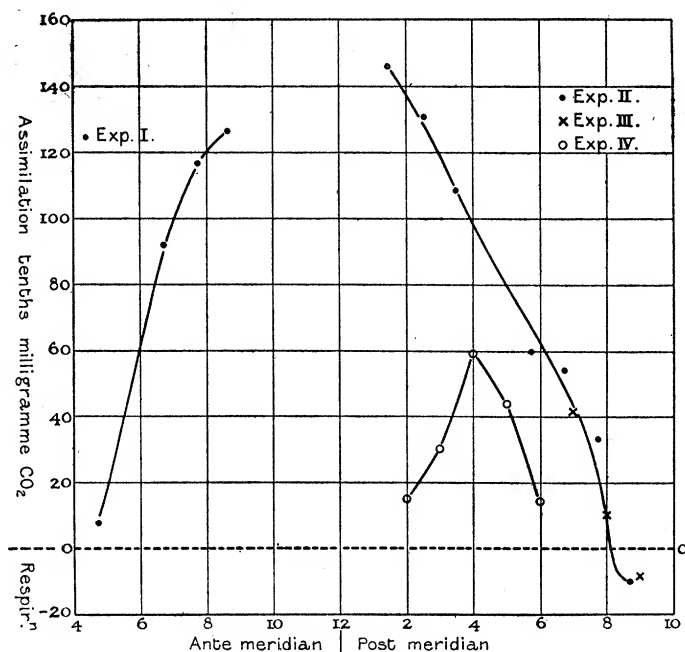The graphic representation, fig. 3, allows us to gather an idea of the rapid

Fig. 3.

mounting up of early morning assimilation. It is not true, however, that the actual amounts are measures of the increase of light. Subsequent work made it probable that the temperature would be the limiting factor in this case, the light being in excess. In Column 5 are given the temperatures for which the observed assimilations are maximal; we find that they agree well with our other experiences of how much such insolation heats up a leaf. The assimilation values are in this case to be taken as a direct measure of the leaf-temperature.

In these early experiments we rather interpret than prove the significance of the assimilation numbers. Direct proof that such and such effects are

due to light or to temperature as limiting factors will be found in later experiments.

Experiment II deals with exposure of a leaf " in the shade " to the collective diffuse light of the sky, the direct sunlight being always cut off by the shadow-board. In this experiment, and in this one alone, the leaf-chamber was not in the bath, but was placed horizontally in the free air with thermometers in contact with it to give a rough idea of the shade-temperature around the leaf. The temperature of a leaf within a chamber in the shade is quite 2° above that of the mercury thermometer (see p. 409). We may thus assume in the first reading the leaf to have been at about 29° C., and we find that the assimilation is maximal for 29°·4 C. (*cf.* p. 413); evidently the diffuse light in the shade is more than enough for an assimilation of 0·0146, but the temperature limits it to that amount. In the second reading the assimilation is a little lower, while in the third reading it is much smaller, and it is clear that this is due to diminution of light, as the

Experiment II (July 13, 1904).—Cherry-laurel; Weight, 1·70 grammes; Area, 54·3 sq. cm.; Current Rate, 800 c.c.; $CO_2 = 2\cdot4$ per cent. (average).

Leaf exposed to Diffuse Light under Shadow-board all Day. Chamber in Air, not in Bath.

Time.	Illumination.	Temperature of air.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
11.45 A.M.—1 P.M.	White cumuli, with gleams of sun	24·9 / 27·0	Preliminary		
P.M. 1—2	,, ,,	27·0	0·0376	0·0137	0·0146
2—3	,, ,, sun 2.20—2.50	27·0	0·0387	0·0123	0·0131
3—4	White cumuli, with gleams of sun	26·6	0·0397	0·0100	0·0110
4—5.15	Mostly sun	26·0			
5.15—6.15	Sun	25·2	0·0376	0·0048	0·0060
6.15—7.15	Sun; cloudless; 6.40, sun below roof	24·3 / 21·9	0·0390	0·0046	0·0054
7.15—8.15	Cloudless; sunset 8.11 ...	21·9 / 19·8	0·0386	0·0027	0·0033
8.15—9.15	Dusk, faint clouds	19·8 / 17·8	0·0367	minus 0·0010	

amount 0·0110 would only be maximal at 24° C. Light is thus falling off faster than the temperature, and has become in its turn the limiting factor; the decreasing assimilation is henceforward a direct measure of the light intensity only.

This series of readings in the waning intensity of afternoon diffuse light is represented graphically in fig. 3, and it will be seen that assimilation is considerable right up to sunset.

The assimilation, of 0·0033, in the last reading but one could have been carried out with a temperature of 7° C. Finally, there is no appreciable light or assimilation, and from 8·15 to 9·15 we get, instead, respiration with an output by the leaf of 0·0010 gramme CO_2.

Experiment III.—The leaf in this experiment was exposed to a natural sequence of irregular illumination throughout the day. The leaf-chamber was inside the water-bath and kept faced normal to the sun (or, when cloudy, to the approximate position where the sun would be) throughout the day. The only interference with the natural sequence of things was an alteration in the temperature of the bath about 4 P.M. The temperature had been kept at about 18° C. by circulating water until 3.35 when heating up (by a primitive and very slow method) was begun. The heating up lasted for two hours, and then the bath slowly cooled down again.

The first three readings—0·0090, 0·0081, 0·0093—are maxima for the temperatures of 21°·0, 19°·1, and 21°·3 C. respectively, and these probably were the average temperatures of the leaf in the respective readings, heated up by the diffuse light and feeble variable sun. Possibly the second reading is really just limited by the dull light. The fourth reading of 0·0067 is clearly so limited as it is well below the maximum even for the bath-temperature. In the fifth reading dull light prevailed at first, but later gave place to sunshine, and the assimilation is 0·0077, a slight increase. During this reading heating up of the bath was begun, but this is not the cause of the rise of assimilation, as 18° C. would have been adequate for what takes place. The sixth and seventh readings both show a large increase due to the improved light, and are a direct measure of this.

In the eighth reading the sun sinks behind a ridge of the roof, and assimilation drops to 0·0043, while there is still appreciable assimilation up to sunset, after which the CO_2 of respiration begins to escape from the leaf.

The values obtained after the sun has gone below the roof are, of course, diffuse light values, and they agree closely with those of Experiment II under the same conditions, as fig. 3 shows.

Experiment III (July 14, 1904).—Cherry-laurel; Weight, 1·75 grammes; Area, 55·1 sq. cm.; Current Rate, 800 c.c.; $CO_2 = 2·5$ per cent. (average).

Leaf-chamber adjusted Normal to Sun throughout the Day.

Time.	Illumination.	Tempera-ture of bath.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
A.M. 9.35—10.35	Bright sunshine	18°·1	Preliminary		
10.35—11.35	Light clouds	{ 18·2 17·4 }	0·0392	0·0089	0·0090
11.35 A.M.— 12.35 P.M. }	Grey clouds; then less dull	{ 17·4 18·7 }	0·0387	0·0079	0·0081
P.M. 12.35—1.35	Sun; cloudy	{ 18·5 18·0 }	0·0415	0·0092	0·0093
1.35—2.35	Mostly sun	{ 18·2 18·8			
2.35—3.35	Dark clouds	18·6	0·0396	0·0064	0·0067
3.35—4.35	Overcast till 4.5; sun	{ 18·5 23·5 }	0·0398	0·0071	0·0077
4.35—5.35	Sun behind chimney; last half hour, sun	{ 23·5 26·6 }	0·0405	0·0103	0·0111
5.35—6.35	Sun through thin cloud ...	{ 26·6 24·4 }	0·0405	0·0100	0·0108
6.35—7.35	Sun below roof; thin cloud	{ 24·4 22·7 }	0·0390	0·0033	0·0043
7.35—8.35	Sunset 8.11	20·0	0·0401	0·0002	0·0010
8.35—9.35	Dusk	18·4	0·0376	{ minus 0·0009	

Experiment IV is the first with a leaf of *Helianthus tuberosus*. This leaf had been set up for an experiment on the previous day with a thermo-junction in it, but owing to trouble with the galvanometer-leads the experiment was abandoned, and re-started the next day with the same leaf still in the chamber.

On this afternoon took place the most violent rain and thunder storm of the year, and assimilation estimations were taken through it. The first reading shows how small is the assimilation, 0·0015, during the gathering of the dense leaden clouds that preceded the storm. A higher number is reached during the bursting of the storm and the slow clearing up.

Experiment IV (July 30, 1904).—*Helianthus tuberosus;* Weight, 1·47 grammes; Area, 70·1 sq. cm. ; Current Rate, 800 c.c. ; CO_2 = 2·5 per cent. (average).

Leaf-chamber faced towards the Approximate Position of the Sun, at Intervals.

Time.	Illumination.	Temperature of bath.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
P.M. 12.30—1.30	—	° —	Preliminary		
1.30—2.30	Heavy leaden clouds; storm drifting up	18·2	0·0426	0·0011	0·0015
2.30—3.30	Violent thunderstorm at first, then slowly clearing up	18·3	0·0384	0·0032	0·0030
3.30—4.30	Brighter; no rain............	18·3	0·0386	0·0073	0·0059
4.30—5.30	Sun at first, then clouded over; storm drifting up	18·3	0·0394	0·0050	0·0043
5.30—6.30	Overcast, steady rain; 6.10, heavy storm	18·0	0·0380	0·0007	0·0010

In the third reading rain ceased, and 0·0059 marks the brighter period. Soon, after a few gleams of sun, a second storm began to drift up, and this burst at the end of the fifth reading. These assimilation values are plotted in fig. 3, and show the passage from one big storm to another through a brighter interval. The assimilation is in no case near the maximum for the temperature, and is a measure of the light only. Possibly the vitality of the leaf has been lowered by prolonged sojourn in the chamber not far from the mercury connecting cups.

We now come to a group of three experiments under the natural sequence of illumination, in which the temperature of the leaf was actually determined thermo-electrically throughout the experiment.

Experiment V took place on a day which was dull up to about 3 o'clock, when the sun came out brightly ; at the same time the temperature of the bath was raised by the circulation of hotter water. The leaf is thus in the last reading both hotter and better lighted than in the first three readings, and there is a marked change in the assimilation.

The first three readings give assimilation values of 0·0073, 0·0065, 0·0077, the average temperature of the leaf being about 20°·5 C. Now, the assimilation

maximum for 20°·5 C. is 0·0088 (see p. 413), from which it follows that the amount of assimilation is not limited by the temperature, but by the dulness

Experiment V (July 22, 1904).—Cherry-laurel; Weight, 1·80 grammes; Area, 55 sq. cm.; Current Rate, 800 c.c.; $CO_2 = 2·4$ per cent. (average).

Leaf-chamber adjusted Normal to Sun throughout the Day.

Time.	Illumination.	Tempera-ture of bath.	Tempera-ture of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
P.M. 11.40—12.40	—	19·0	—	Prelim	inary	
12.40—1.40	Dull, cloudy sky ...	19·0	20·5	0·0392	0·0070	0·0073
1.40—2.40	,, ,, ...	18·8	20·0	0·0384	0·0062	0·0065
2.40—3.10	Clouds less heavy...	19·2	21·1	0·0192	0·0037	0·0077
3.10—3.40	Sun coming out ...	Heated to 29·0				
3.40—4.25	Bright sun for most of estimation	{ 29·0 { 26·3	Variable, 35·8—31·5	} 0·0368	0·0132	0·0190

of the illumination. In the final reading the value obtained, 0·0190, is the standard maximum for 33°·7 C.,* which is about the average observed temperature of the leaf. Here, then, the assimilation, in spite of its magnitude, is yet limited by the temperature and not by the light, which is quite superfluously bright (as will be precisely demonstrated in Section V).

It is interesting to note that the excess of the leaf-temperature over the bath-temperature gives a rough measure of the intensity of the incident light-radiation. The successive values 1°·5 C., 1°·2 C., 1°·9 C., and 5°·2 to 6°·8 C., vary parallelly with the assimilation.

Experiments VI and VII exhibit mixed effects of varying illumination and temperature, and frequent records of both were taken in order to see how far the assimilation values could be explained in detail by these data. We will take first Experiment VI, in which each reading lasted an hour, and the temperature and illumination were noted every 10 minutes. The details of these are given in the schedule of the experiment, and graphically in fig. 4 The significant averages are given in Table I on p. 424.

The day was dull and cloudy; continuous sun about 2 to 3 P.M. only. The assimilations fall short of maximal throughout the day. As the chamber was

* Or for 33° C., as this is an early reading; see p. 412 on influence of "time factor."

faced to the south, and left unmoved all day, the afternoon bright sun fell on it obliquely, and did not produce its full effect.

Experiment VI (July 24, 1904).—Cherry-laurel; Weight, 1·90 grammes; Area, 62·6 sq. cm.; Current Rate, 800 c.c.; $CO_2 = 2\cdot4$ per cent. (average).

Leaf faced to South; Position unchanged throughout Experiment.

Time.	Illumination.	Temperature of bath.	Temperature of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
A.M. 8.30—9.30	Dull, cloudy day ...	° —	° —	Preliminary		
9.30—10.30	Alternate sun-gleams and dull	{ 18·8 19·4 }	} 23·5	0·0403	0·0100	0·0092
10.30—11.30	Dull till 11, then faint sun	{ 19·2 20·2 }	} 23·2	0·0413	0·0103	0·0095
11.30 A.M.— 12.30 P.M.	Gleams of sun till 12, then dull	{ 20·6 19·5 }	} 23·8	0·0431	0·0111	0·0102
P.M. 12.30—1.30	Uniformly dull	19·7	21·4	0·0410	0·0076	0·0071
1.30—2.30	Bright sun throughout	20·4	26·9	0·0360	0·0114	0·0108
2.30—3.30	Bright sun, except at 2.50, when clouds	20·7	26·3	0·0367	0·0098	0·0093
3.30—4.30	Bright at beginning and at end; dull in middle	19·9	21·8	0·0366	0·0062	0·0061
4.30—5.30	Sun at first, then thin cloud	20·0	21·5	0·0372	0·0054	0·0054
5.30—6.30	Bright sun; sun and thin cloud	{ 19·8 19·7	20·4 19·9	} 0·0365	0·0040	0·0041

The three first readings have about the same illumination-intensity; witness the uniform leaf-temperature and uniform excess of leaf-temperature over bath-temperature. As the scattered gleams of sun fall on the leaf with decreasing angle of incidence, so the assimilation rises from 0·0092 to 0·0102, and gets practically to be maximal for the third reading. In the fourth reading a long period of very dull sky brings the assimilation down to 0·0071. After that, continuous sun gives the highest assimilation of the day, and the highest excess of leaf-temperature, though a still larger assimilation would be expected. From that point the light steadily becomes feebler, and that part
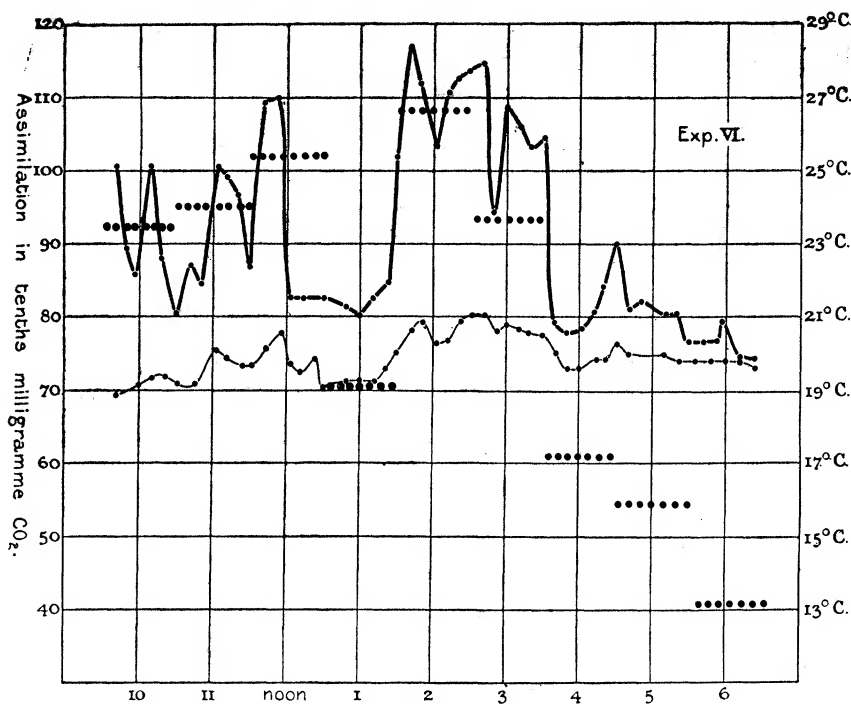
Fig. 4.

The heavy line connects the successive leaf-temperatures; the light line the corresponding bath-temperatures. The horizontal lines of dots indicate the assimilation in successive hours.

Both the temperature-curves show fluctuations according as the sun is clear or clouded, but these are much more violent in the leaf than in the large mass of water in the bath, which is continually being replaced by running water of fairly uniform temperature.

From inspection of the graphic record of the bath-temperature, one can learn when the sun was shining and when clouded; from the graphic of the leaf-temperature a more detailed reconstruction of the sequence of illumination is possible, while the *difference* between the two temperatures gives information of considerable precision about the intensity of illumination; this is used in Tables I and II.

Table I.—Experiment VI.

No. of estimation.	Hour.	Excess temperature of leaf.	Observed leaf-temperature.	Maximal assimilation for observed temperature.	Observed assimilation.	Deficiency of observed assimilation.
1	10	4·3	23·5	0·0106	0·0092	− 14
2	11	3·6	23·2	0·0104	0·0095	− 9
3	noon	4·1	23·8	0·0108	0·0102	− 6
4	1	1·9	21·4	0·0093	0·0071	− 22
5	2	6·4	26·9	0·0127	0·0108	− 19
6	3	5·6	26·3	0·0123	0·0093	− 30
7	4	2·0	21·8	0·0095	0·0061	− 34
8	5	1·5	21·5	0·0094	0·0054	− 40
	6	0·6	20·2	0·0086	0·0041	− 45

of it due to direct sunlight becomes more and more obliquely incident, so that the leaf-excess-temperature falls from 5°·6 to 0°·6 C., bringing a steady fall of assimilation. The bath is, however, kept up to about 19° C. by circulating water, so that the leaf-temperature cannot fall as fast as the illumination, and the assimilation shows a larger and larger deficit below the maximum. The whole experiment exhibits the assimilation as a function of the illumination, and not limited by the temperature.

Experiment VII, on the contrary, shows the assimilation as a function of the temperature; it was a brighter day, and the leaf-chamber was continually adjusted normal to the sun's rays.

Experiment VII (July 23, 1904).—Cherry-laurel; Weight, 1·72 grammes; Area, 52·5 sq. cm.; Current Rate, 800 c.c.; $CO_2 = 2·1$ per cent. (average).

Leaf-chamber adjusted Normal to Sun throughout Day.

Time.	Illumination.	Temperature of bath.	Temperature of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
A.M. 8.20—9.20	—	°	°	Preliminary		
9.20—9.50	Fairly bright sun ...	19·3	25·0	0·0165	0·0054	0·0117
9.50—10.20	10.3—10.9, heavy cloud; 10.12, bright sun; then dull	18·5 18·9 18·8	21·2 21·9 21·3	0·0172	0·0045	0·0095
10.20—10.50	10.27, faint sun; 10.36, bright sun; 10.42, brilliant sun	19·0 19·6 20·1	22·2 27·2 29·2	0·0181	0·0052	0·0115
10.50—11.20	11, bright sun; 11.15, cloudy	20·1 19·6	30·1 23·7	0·0180	0·0052	0·0115
11.20—11.50	Cloudy..................	19·1	22·3	0·0181	0·0042	0·0091
11.50 A.M.—12.20 P.M.	Heavy clouds	19·2	21·3	0·0146	0·0041	0·0088
P.M. 12.20—12.50	Heavy clouds	19·3	20·6	0·0184	0·0036	0·0076

The readings only last half an hour each, and the temperature and illumination were recorded every three minutes throughout the experiment, so that full data for a careful analysis are available. The following table exhibits the significant numbers and averages :—

Table II.—Experiment VII.

1. Middle hour of estimation.	2. Difference between calculated and observed temperatures, 4 *minus* 3.	3. Leaf-temperature calculated from assimilation (data on p. 413).	4. Average observed leaf-temperature.	5. Observed assimilation.	6. Assimilation maxima for observed temperature (data on p. 413).	7. Difference, 5 and 6.	8. Excess leaf-temperature over bath.
9.35	$-0°\cdot3$	$25°\cdot3$	$25°\cdot0$	0·0117	0·0115	+ 2	$5°\cdot7$
10.5	$-0\cdot2$	21·6	21·4	0·0095	0·0094	+ 1	2·5
10.35	$+0\cdot9$	25·0	25·9	0·0115	0·0120	− 5	5·7
11.5	$+1\cdot2$	25·0	26·2	0·0115	0·0122	− 7	5·2
11.35	$+1\cdot3$	21·0	22·3	0·0091	0·0099	− 8	2·9
12.5	$+0\cdot8$	20·5	21·3	0·0088	0·0093	− 5	2·3
12.35	$+2\cdot5$	18·1	20·6	0·0076	0·0088	−12	1·3

In the last reading the sky is heavily overcast, the excess leaf-temperature and the observed assimilation the smallest recorded. The light is obviously the limiting factor, and the assimilation well below the maximum.

In the other readings the observed assimilation is close to that calculated as maximal from the observed leaf-temperature. The table is designed to show how closely one can calculate the leaf-temperature from the observed assimilation, viz., Column 3 from Column 5, the error being given in Column 2; and also, inversely, calculate the assimilation from the temperature, viz., Column 6 from Column 4, the error being in Column 7.

The temperature error (omitting the last reading) averages only $0°\cdot8$ C., and the assimilation error 0·0005 gramme CO_2. It is to be noted that there are no "preliminaries" between the different readings, so that the effects here tend to run into one another.

The relation of temperature and assimilation is exhibited as an extraordinarily constant one when one recalls that the temperature maxima used in the calculation are derived from experiments made at a different season of different years, and with artificial light.

Section IV.—*Illumination and Temperature as "Limiting Factors" in Assimilation.*

We now pass to the consideration of some experiments which are not merely records of the hourly march of natural illumination and temperature, but in which the conditions are manipulated to bring out certain points.

In Experiment VIII the leaf was for the first three readings exposed only to the diffuse light of a brilliant cloudless day. The sun's direct rays were throughout intercepted by the shadow-board, and the readings show the slow

falling-off, characteristic of the afternoon diffuse light. The temperature of the bath was 30° C., and that of the leaf would be about 32°. The absolute amounts of real assimilation in the first three readings 0·0122, 0·0118, 0·0109, are such as would be maximal for the temperatures of 26° C., 25°·5 C., 24° C.; the diffuse light is evidently, though adequate for the possible assimilation at these temperatures, not adequate for that at 32°. To provide evidence in this direction, the shadow-board was removed at 3.30, and the leaf adjusted normal to the sun's rays, when the assimilation at once went up to nearly double, *i.e.*, to 0·0200. The bath became 1° hotter and the leaf would be heated 5° to 6° C. higher still by the sun's direct radiation, so that in substantial harmony with this we find the new amount of assimilation to be that maximal for 34°·6 C., or for a degree or two higher when allowance is made for the fact that the heating has been prolonged for four hours: at this temperature the time factor is not negligible.

Experiment VIII (July 18, 1904).—Cherry-laurel; Weight, 1·98 grammes; Area, 60 sq. cm.; Current Rate, 800 c.c.; $CO_2 = 2·4$ per cent. (average).

Exposure.	Time.	Illumination.	Temperature of bath.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
Leaf-chamber exposed to diffuse light only Shadow-board	11.30 A.M.— 12.30 P.M.	Cloudless, thin haze over sun	30°·2	Preliminary		
	P.M. 12.30—1.30	,,	30·1	0·0375	0·0115	0·0122
	1.30—2.30	,,	30·1	0·0392	0·0111	0·0118
	2.30—3.30	,,	30·1	0·0362	0·0100	0·0109
3.30 P.M., leaf exposed to sun *plus* diffuse light	3.30—4.30	,,	31·1	0·0350	0·0197	0·0200

The assimilation-value in the diffuse light is here an exact measure of its intensity, as the temperature is not limiting. It is thus proved not to be very intense, which is due to the fact that the day was cloudless, and but little sun was therefore reflected by clouds into the "shade." A distinctly higher value 0·0146 was obtained in Experiment II, and even that was limited by the temperature of 29° C., while in the next experiment a very much higher value is obtained on a day with abundant white cumuli.

Experiment IX.—In this experiment with *Helianthus* the temperature of

Experiment IX (August 7, 1904).—*Helianthus tuberosus*; Weight, 1·20 grammes; Area, 53·3 sq. cm.; Current Rate, 800 c.c.; CO_2 = 5·8 per cent. (average).

Exposure.	Time.	Illumination.	Temperature of bath.	Temperature of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
Leaf exposed to small patch of diffuse skylight through wooden tube	A.M. 8.30—10	Close white cumuli	{ 29·2, 29·8	{ 29·5	Preliminary		
	10—10.30	Mostly cloudy	{ 29·2, 29·8	29·5	0·0453	0·0019	0·0053
Tube removed, shadow-board, full diffuse light	10.30 A.M.— 12.30 P.M.	—	29·0	30·0			
	P.M. 12.30—1	Bright sun with cumuli	29·2	{ 30·0, 31·0	0·0503	0·0102	0·0212
Leaf adjusted normal to sunlight only; wooden tube	1—2	Bright sun, a few clouds	—	{ 30·0, 31·0			
	2—2.15	Bright sun (1 min. cloud)	—	{ 29·0, 30·0	0·0255	0·0042	0·0177
	2.15—3.2	Cloudy					
	3.2—3.42	Good sun (3 mins. cloud)	—	{ 29·0, 30·0	0·0708	0·0126	0·0195
Bath darkened	5.50—7.15	Dark	29·5	29·5	CO_2 free	CO_2 respired	
	7.15—8.15	,,	29·5	29·5	—	0·0018	
	8.15—9.15	,,	29·5	29·5	—	0·0020	

the leaf was directly determined thermo-electrically, and an attempt was made to keep the leaf-temperature uniform by altering the temperature of the water circulating through the bath. When the leaf has to be exposed to direct sun then the gas-supply to the water-heater is diminished, or the rate of water circulation is increased, so as to compensate for the warming up produced by direct insolation.

This was a bright day, on which the sky was more or less closely packed with brilliant white cumuli.

For the first reading the wooden tube was fitted on to the bath and the tube pointed, not towards the sun but to a part of the sky away from the sun and nearer the zenith. A comparatively small number, 0·0053, was obtained (but not so small as expected), corresponding to the patch of diffuse light that finds its way down the tube. The second reading is taken in full diffuse light behind the shadow-board, and reaches the high value of 0·0212. This, as might well be expected, represents the full effect of the light, and is not limited by the temperature; Curve A in fig. 2 shows that a very much larger assimilation would be possible at this temperature. Then several readings in direct sunlight only are taken by replacing the wooden tube and keeping it pointed to the sun. The assimilation of 0·0177 in the first of these readings is much smaller than the one in diffuse light, but subsequently a more nearly equal reading of 0·0195 (or, allowing for the three minutes of cloud, 0·0209) is obtained. This whole experiment shows how efficient total diffuse sky-light may be in relation to poor direct insolation alone.

The weather broke up at 3.42, and so two estimations of the respiration in the dark were made, and the values here obtained at 29°·5 C. are part of the data for the respiratory curve in fig. 2.

In Experiment X with *Helianthus* the leaf-temperature was, for most readings, kept much lower, and it will be seen that therefore the amounts of assimilation are limited by the temperature. Rain fell on and off throughout the day, and no sun appeared till the last reading at 3.42 P.M. The chamber faced south and 30° above the horizon throughout the day, unmoved, thus receiving a large amount of diffuse light from the sky. When the sun appeared for the last reading the shadow-board was used to intercept its rays. The whole experiment then is conducted in diffuse light of varying brightness.

For the first four readings the temperature was kept down to about 18° C., and, again, in the last two the temperature was the same. In all these readings except the first, which was low, due to the extremely overcast leaden sky, the assimilation numbers are remarkably uniform, 0·0089, 0·0090, 0·0089, 0·0089, 0·0092; while the light varied up and down, being especially brighter in

Experiment X (August 11, 1904).—*Helianthus tuberosus;* Weight, 1·20 grammes; Area, 61·2 sq. cm.; Current Rate, 800 c.c.; $CO_2 = 4$ per cent. (average).

Leaf-chamber stationary all Day, facing South, elevated 30°.

Time.	Illumination.	Temperature of bath.	Temperature of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
A.M. 9.30—10.30	Very overcast	—^{c}	—^{o}	Preliminary		—
10.30—11	,, ...	—	17·7	0·0362	0·0034	0·0062
11—11.30	Raining, but lighter	17·0	18·0	0·0362	0·0050	0·0089
11.30—noon	Raining, lighter still	17·1	18·0	0·0377	0·0051	0·0090
P.M. noon—12.30	Raining, heavy clouds	17·0	17·7	0·0390	0·0050	0·0089
1.10—2.20	Raining	{ Heated 29·8				
2.20—2.50	,, ...	29·8	30·5	0·0240	0·0087	0·0163
2.50—3.12	No rain, lighter	{ Cooled 16·6				
3.12—3.42	Much brighter	16·6	18·2	0·0235	0·0050	0·0089
3.42—4.12	Sun out, but leaf shaded by the shadow-board	16·6	18·4	0·0254	0·0052	0·0092

the last two readings. This can only be interpreted as being due to the fact that the assimilation is limited by the temperature, which has been kept steady throughout.

Striking confirmation of this is obtained by raising the temperature for the fifth reading. The sky was no lighter than before, but yet, on the temperature being brought up to 30·5, the assimilation at once doubled, becoming 0·0163. This number will then be the exact expression of the intensity of the illumination only, for an assimilation of at least 0·0289 is possible at this particular temperature.

Nothing could show better than this experiment the impossibility of investigating the effect of varying illumination while ignoring the leaf-temperature.

In Experiment XI with *Helianthus*, the temperature of the bath was varied up and down several times for alternate pairs of readings, and careful records of the temperatures of the leaf and of the bath were made every 10 minutes, or less, according to the variability of the insolation.

Experiment XI (July 28, 1904).—*Helianthus tuberosus;* Weight, 1·96 grammes; Area, 71·2 sq. cm.; Current Rate, 800 c.c.; $CO_2 = 2\cdot4$ per cent. (average) till 3.10 P.M., and 5·0 per cent. (average) after 3.10 P.M.

Leaf-chamber adjusted Normal to Sun throughout the Day.

Time.	Illumination.	Temperature of bath.	Temperature of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
A.M. 9.15—10.40	Heavy cumuli.........	° —	° —	Preliminary		
10.40—11.10	10.48, thin cloud; 10.52, slight rain; 11, cloud haze	19·5 18·1	22·7 22·0	0·0183	0·0086	0·0131
11.10—11.40	11.10, cloud haze; 11.30, heavy cloud	18·0 17·7	20·8 20·6	0·0192	0·0072	0·0109
11.40 A.M.— 12.10 P.M.	11.40, bright sun; 12, cloud haze	Heated 26·4 27·2	35·0 31·0			
P.M. 12.10—12.40	12.10, sun; 12.25, faint sun; 12.30, faint sun	27·8 28·1 28·4	33·8 30·5 29·4	0·0191	0·0180	0·0275
12.40—1.10	12.40, sun; later overcast	28·0 27·9 28·5	32·0 29·6 28·4	0·0191	0·0117	0·0184
1.10—1.40	Bright sun; 1.30, faint sun	Cooled 18·3 17·9	24·4 21·6			
1.40—2.10	1.40, thin cloud; 1.50, dull; 2, bright sun	17·7 17·6 17·7	21·4 22·6 22·2	0·0194	[0·0110	0·0166]
2.10—2.40	2.10, faint sun; 2.30, faint sun	17·6 17·3	22·6 21·8	0·0195	0·0084	0·0128
2.40—3.10	2.44, sun; 2.52, thin cloud	Heated 23·8 27·6	29·4 28·2	0·0200		
3.10—3.40	3.12, faint sun; 3.31, light sun	27·2	28·8 29·6	0·0290*	0·0145	0·0222
3.40—4.10	—	Gas out	—	0·0350	—	—
4.10—4.40	4.30, faint sun.........	Cooled 18·9 17·6				
4.40—5.10	Thick cloud............	17·9 17·2	17·8 17·6	0·0345	0·0055	0·0084
5.10—5.40	Cloudy.................	Heated 25·6 28·6	29·2 29·0			
5.40—6.10	Cloudy.......	28·7 28·4	29·4 28·6	0·0332	0·0038	0·0071

* CO_2 supply increased, previously insufficient, see third reading.

Both temperatures are plotted in fig. 5, and the difference between them gives a measure of the intensity of the solar radiation at any time.

Several errors and mishaps vitiate the middle part of this experiment, but it is, nevertheless, valuable; there is a very instructive difference between the effect of raising the temperature near noon, when the light is strong and the temperature limiting, and of again raising it late in the afternoon, when the light itself is limiting.

In the first two readings the bath-temperature is about 18° C., and the leaf-temperature 4° to 2°·5 higher, giving, firstly, 0·0131 at the average temperature of 22°·2 C., and secondly 0·0109 at 20°·7 C. The day is now bright, though not clear of clouds. The light is much in excess of the above values, and they are taken as maximal for their respective temperatures (see fig. 2). They fall into one curve with the value of 0·0090 at 18° C. obtained in Experiment X.

After these two readings hotter water was circulated through the bath to give a temperature of about 27° C. The sun was irregular, and its outbursts show clearly on the temperature records, the leaf responding more acutely than the bath. The value 0·0275 was recorded at 31°·2 C. This large number is not, however, maximal, though the light is bright enough, and it was undoubtedly limited by a quite unusual factor—the CO_2 supply. Not anticipating such vigorous assimilation, we had only provided 0·0191 gramme CO_2 per half-hour, and the table shows that the leaf had absorbed as much as 0·0180. There is thus quite an inadequate margin of supply, and presently the CO_2 was increased. The fourth reading falls into quite dull illumination, as the closeness of the two temperature curves shows, and is no doubt limited by the light, giving only 0·0184 at 30° C. (*cf.* fig. 5).

After these readings the bath was cooled again. The fifth reading must be due to an undetected error of some sort, for it appears to be much *above* the maximum for the recorded temperature, while the sixth is normal again, and just about the same as the first, in temperature and assimilation, though light is much brighter and temperature-difference is large. Then a second time the bath is heated up and the assimilation rises to 0·0222 at 29° C. The next reading is spoilt by a drop in the temperature due to accidental extinction of the gas of the water-heater.

Once more the bath is cooled down, and as the sky is thickly clouded the temperature-difference is now very small. The assimilation, 0·0084, is a little below the maximum for 17·7, and the light should be the limiting factor. This is made evident by heating up again for the last time, when in spite of a return to the temperatures about 29° C., there is, in contrast, no rise of assimilation, but a further fall with the decreasing light, which also reduces considerably the temperature-difference.
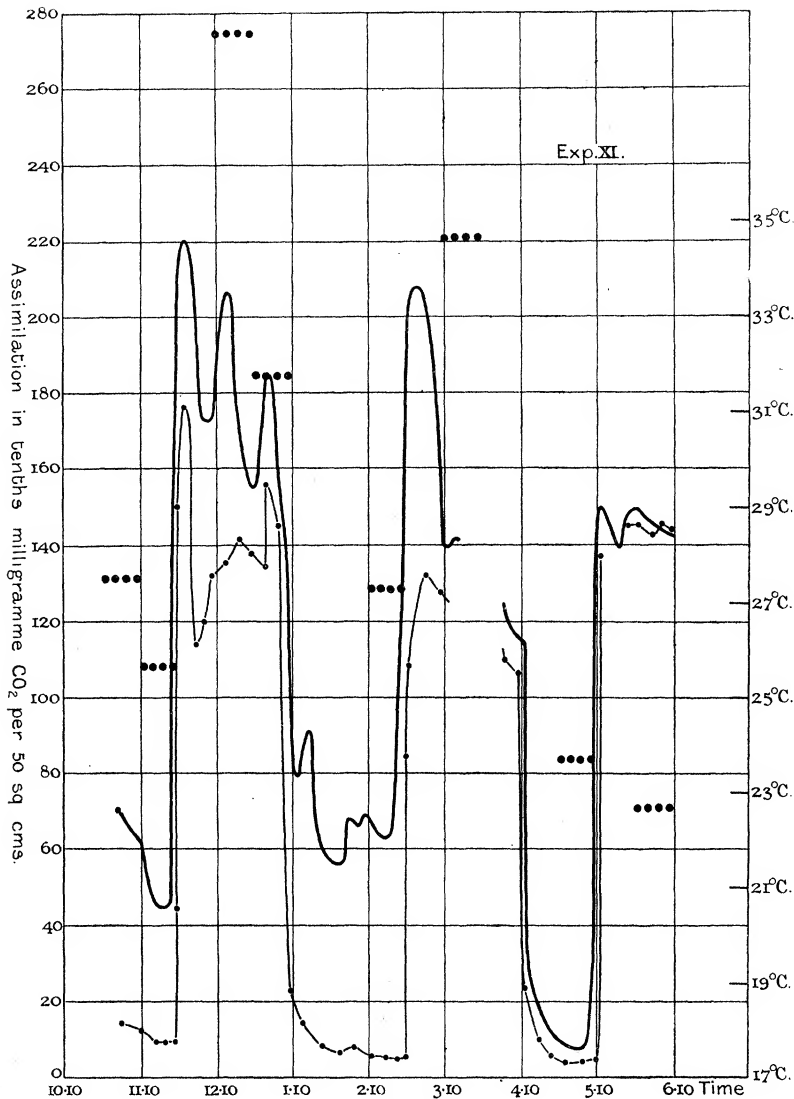
FIG. 5.

Explanation as in fig. 4, p. 424.

The contrast between the effect of the last heating and the effect of the first two heatings is very marked in the figure.

Experiment XII is an interesting example of the extremely rare case of a leaf that has temperature-maxima departing conspicuously from the standard maxima. It was cut from a shrub of cherry-laurel growing in a pot, not from the garden shrub used for all the other published experiments, but other leaves of this pot-plant gave normal numbers. Its behaviour is governed by the same

principles as that of normal leaves, but it is more feeble throughout; it is instructive to note that its maxima at 26° C. and 32° C., viz., 0·0103 and 0·0139, bear such a ratio to one another as to indicate that this leaf has a somewhat smaller coefficient of temperature acceleration than a normal leaf. If so, the feeble leaf would differ from normal cherry-laurel leaves in just the same way as the latter differ from leaves of *Helianthus* (*cf.* Section VI).

Experiment XII (August 1, 1904).—Cherry-laurel; Weight, 1·79 grammes?; Area, 60 sq. cm.; Current Rate, 800 c.c.; $CO_2 = 2·1$ per cent. (average).

Exposure.	Time.	Temperature of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
Leaf exposed to whole diffuse light *plus* half sunlight (angle incid. = 60°)	A.M. 9—10	26·2	Preliminary		0·0103
	10—10.30	26·0	0·0318	0·0053	
	10.30—11 {	Heated 32·0			
	11—11.30	32·0	0·0308	0·0063	0·0131
Whole diffuse light *plus* whole sunlight (angle incid. = 0°)	11.30—noon	32·0			
	noon—12.30 P.M.	32·0	0·0320	0·0068	0·0139
Whole diffuse light *plus* half sunlight (angle incid. = 60°)	P.M. 12.30—1	32·0			
	1—1.30	32·0	0·0350	0·0064	0·0133

This leaf was so placed at first that the sun's rays fell on it obliquely with an angle of incidence = 60°, *i.e.*, the sunlight was of only half its full intensity; the collective diffuse light fell on it unimpeded. When the leaf-temperature was 26° C. the assimilation was only 0·0103 instead of 0·0121 (the normal maximal value for 26° C.). The day was very bright and sunny, and this clearly is the maximum for the temperature. That this is so was proved in the second reading when, with the same intensity of light (the chamber being continually readjusted to the angle of 60°), raising the temperature of the bath sent the assimilation up 25 per cent.

At about 32° C. the value obtained is 0·0131, very nearly or approaching maximal. Next the light is in its turn increased by adjusting the chamber normal to the sun's rays so as to double their intensity, and the temperature is kept down still to 32° C. There is only a small increase of assimilation and that may possibly only be due to unrecorded increase of temperature.

This failure to show a marked increase with marked increase of light proves that the assimilation is limited by the temperature of 32° C. For the last reading the light is diminished again, while the temperature is maintained and there is no serious fall in the assimilation.

The assimilation values are then throughout limited by the temperature in the same manner as with normal leaves, and we have in one experiment the two instructive cases of (1) increase of light with stationary (limiting) temperature not causing increase of assimilation, and (2) increase of temperature with stationary (non-limiting) light causing increase of assimilation.

Section V.—*The Photosynthetic Value of Full Insolation.*

In this section we propose to give further precision to our knowledge of the relation of temperature and illumination to assimilation. We propose to ascertain what amounts of illumination correspond to certain assimilation maxima, in other words to measure the amount of assimilation corresponding to definite intensities of insolation.

The procedure consists in experimenting with exactly known fractions of full midday sunlight.

Various methods have been used for reducing the intensity of sunlight to a known extent. We made a few experiments with a method based on varying obliquity of incidence of the light and also with one employing different positions in the diverging cone of light from a condenser-lens. These could not be accurately applied without elaborate adaptation. The "photometer-wheel"[*] of rotating sectors can be used to transmit any desired fraction of total incident light, but seems inadmissible for such work as ours because it fractions the light *in time* and not *in intensity*. If set to half opacity it allows the full intensity of light to pass for half the time, and when rapidly rotating this gives *to the human eye* an impression of steady light of half intensity. For an assimilating leaf it would give only illusory results except when the light was a "limiting factor." Thus if, in a particular case, a leaf were limited by its temperature to using just 50 per cent. of the total sunlight, then halving the actual intensity should not diminish the assimilation (provided of course that the temperature were kept up), while halving this total illumination in time should reduce the assimilation to one-half.[†]

Finally, we made use of the ideally simple method of employing fractioning screens made of thin metal plates perforated with holes.[‡] These were placed across the mouth of the 4-foot tube directed towards the sun, that had been

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[*] See Abney, 'Phil. Trans.,' 1887, and Langley, 'Phil. Mag.,' 1889, vol. 27.

[†] See, however, Note B, p. 459.

[‡] Our attention was directed to these by Professor Liveing.

used to cut off the diffuse sky-light from the leaf. Different specimens of commercial wire gauze and perforated zinc were employed, and the area of their perforations and the distances of these apart were measured with a microscope. The total percentage of opening was thus obtained and the percentage of sunlight transmitted would be the same. At a distance of 4 feet these screens, the holes in which were less than 3 mm. in diameter, cast a perfectly uniform field of light. Since the sun's disk subtends a sensible angle ($0°$ $32'$) at the earth's surface, a diverging cone of rays will be transmitted through each perforation. These cones soon interpenetrate and give a more and more uniformly lighted field the further the illuminated object is from the screen. With perforations 3 mm. in diameter the fully insolated points die out at 33 cm. from the screen, and at less than four times this distance no lack of uniformity of illumination can be detected by the eye.

For the fractions obtained to be of any precise significance, the initial sunlight must be of approximately the same intensity in the various cases, so that only unclouded weather within the hours close to the middle of the day is available. We have consequently had to make a number of unsuccessful attempts before the required data could be collected. In some cases a reading has had to be interrupted in the middle while a single cloud drifted up across the sun, and has been taken up again when the cloud has gone, allowing, of course, sufficient interval for the passing away of the effect of the momentarily diminished assimilation on the CO_2-content of the current. When a reading has been obtained in this way it will be stated.

We propose to determine first what fraction of full sunlight must be incident upon a leaf of cherry-laurel to enable it to carry out its maximal assimilation at $29°·5$.

Experiment XIII, August 9.—The chamber was in the first instance faced to the sun, and received full intense sunlight together with the diffuse light of a cloudless sky. In the first reading, 9.30 to 10 A.M., the assimilation is $0·0152$ gramme per hour, at an average leaf-temperature of $29°·7$ C. The temperature of the leaf was taken a number of times during this and subsequent readings, and was always kept adjusted close to the average given, by altering the temperature of the water circulation. With this intense illumination the assimilation must be maximal, and the value is just above the standard maximum for $29°·7$, i.e., $0·0148$, due to this being an early reading.

For the second reading the wooden tube is put on to the chamber, so that the leaf receives only direct sunshine without the general diffuse light. The assimilation is, however, not lowered (but, as it happens, a trifle larger) by the

Experiment XIII (August 9, 1904).—Cherry-laurel; Weight, 1·78 grammes; Area, 56·2 sq. cm.; Current Rate, 800 c.c.; CO_2 = 5·8 per cent. (average).

Exposure.	Time.	Illumination.	Temperature of bath.	Temperature of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
Leaf normal to sun *plus* diffuse light	A.M. 9—9.30	Intense sun, cloudless	20·9°	28·5°	Preliminary		
	9.30—10	„	22·1	29·7	0·0437	0·0073	0·0152
Leaf normal to sun only, with tube	10—10.18	„	22·3	29·2	0·0450	0·0074	0·0154
	10.18—10.48	„	22·3	29·5			
Leaf in diffuse light only; shadow-board	10.48—11.48	Clouding over.					
	11.48 A.M.—12.20 P.M.	Very little sun, heavy white cumuli	—	29·1			
	P.M. 12.20—12.50	„	—	29·1	0·0487	0·0065	0·0136
Chamber darkened for respiration estimations	2.45—4	Darkened	30·0	30·0	—	Respiration	
	4—5	„	30·0	30·0	—	0·0021	
	5—6	„	30·0	30·0	—	0·0024	

diminution of light, because it is in both cases limited by the temperature to the maximal value.

As the sky then began to cloud up it was impossible to employ the fractioning screen, and a reading was therefore taken of the effect of diffuse light only, removing the sun-tube, and putting up the shadow-board. With this illumination we got an assimilation of 0·0136 at 29°·1 C., which is a trifle below the standard maximum for the temperature, 0·0143, which may well be due to the decline after three hours' maximal assimilation at this fairly high temperature.

These values are plotted with crosses in fig. 6, where the lower dotted line represents the curve of assimilation falling off with the time-factor from the hypothetical initial value of 0·0167, through the standard value of 0·0148 (after about two hours), to the observed value of 0·0136 after three and a half hours.

Apart from the time factor it is obvious that all three kinds of illumination —diffuse light alone, direct sun alone, and direct sun *plus* diffuse light—are producing practically the same amount of assimilation, not, of course, because they are equal in intensity, but because the assimilation is limited by the temperature, all the lights being in excess.

Having by this experiment got full evidence as to the magnitude of the assimilation maximum at 29°·5 C., the next experiment was planned for a fraction of the sunlight. A piece of gauze was employed that transmitted 0·62 of the whole incident light.

In Experiment XIV the leaf was set up at 9.15 ; the day was cloudless, but with a thin haze. As the haze obstinately remained, the chamber was darkened for two hours. Then at 11.25, the haze being nearly gone, the wooden tube was put on with the 0·62 screen, and this kept pointed to the sun. An estimation at noon gave 0·0154, just the theoretical value as shown in fig. 6, and maximal for the leaf-temperature, showing that even 0·62 sunlight is more than sufficient for maximal assimilation at 29°·5 C.

Heavy clouds came up soon after this reading, and the experiment was abandoned, and the next one was made with a piece of perforated zinc with much smaller holes, and transmitting 0·28 sunlight.

In Experiment XV a leaf was set up by 9 A.M. ; the day was brilliantly sunny, with large, but very remote, cumuli drifting slowly across the sky. At 10.14, after a long cloudless spell, it seemed that an estimation might be started, but this had to be interrupted in the middle for the passage of one big cloud across the sun. At the moment of eclipse the current was shifted by hand back into the preliminary tube, and kept there for 20 minutes after the cloud had passed, and then it was returned to the estimation tube. At

Experiment XIV (August 13, 1904).—Cherry-laurel; Weight, 1·48 grammes; Area, 49·0 sq. cm.; Current Rate, 800 c.c.; CO_2 = 5·8 per cent.

Exposure.	Time.	Illumination.	Temperature of bath.	Temperature of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
Leaf darkened	A.M. 9.15—11.25	Hazy	°	°	Preliminary		
	11.25—11.50	Haze melting	—	29·0			
Leaf exposed to 0·62 sunlight with tube	11.50 A.M.— 12.20 P.M.	Cloudless sunshine...	27·0	28·7—30·4	0·0452	0·0065	0·0154

Experiment XV (August 16, 1904).—Cherry-laurel; Weight, 1·78 grammes, Area, 56·0 sq. cm.; Current Rate, 800 c.c.; CO_2 = 6 per cent. (average).

Exposure.	Time.	Illumination.	Temperature of bath.	Temperature of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
Leaf exposed to 0·28 sunlight with tube	A.M. 9—10.14	Very bright sun, occasional clouds	28·5	29·7	Preliminary		
	10.14—11.8 32 mins. sun	,, ,,	28·3	29·4	0·0492	0·0058	0·0116
Leaf exposed to full sunlight with tube	11.8—11.45	Very bright sun, no clouds	22·1	29·8			
	11.45 A.M.— 12.15 P.M.	,, ,,	22·1	29·6	0·0467	0·0068	0·0141

11.8 a second cloud came up, and the reading was ended, having consisted in all of 32 minutes of brilliant sunshine. The assimilation per hour with 0·28 sunlight was 0·0116 for 29°·4 C., distinctly less than 0·0147, the maximum
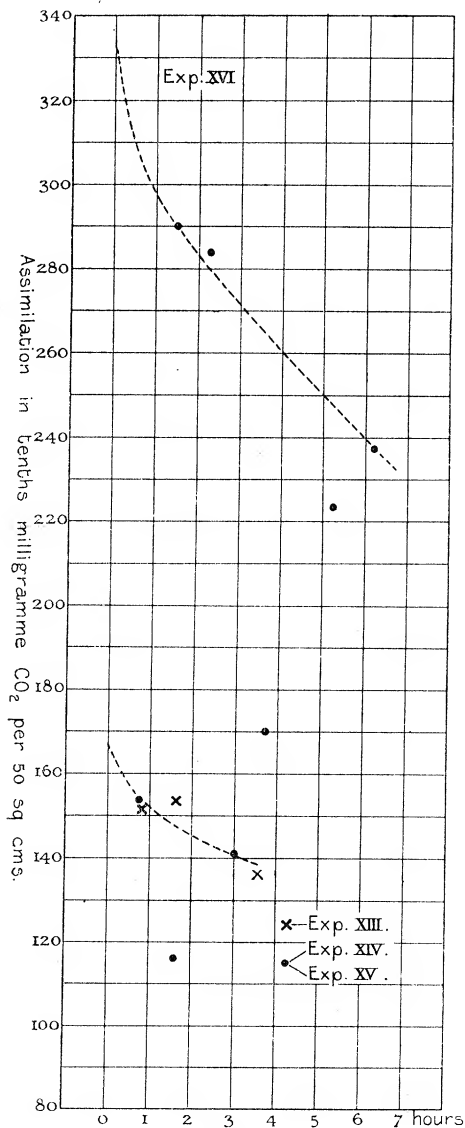

FIG. 6.

which the temperature should allow. The metal screen was then removed, and a reading in full sunshine obtained, which gave the value of 0·0141 at 29°·6, which is just the value we should expect after three hours' high assimilation.

These data are plotted in fig. 6, where the line from 0·0167 to 0·0140 represents the fall of the assimilation maxima at 29°·5 due to the time-factor.

We see from this, that at 10.30 A.M., $1\frac{1}{2}$ hours *ab initio*, we should expect a value of 0·0148. With 0·28 sunlight at this time in Experiment XV we get a value of 0·0116—*i.e.*, 0·28 sunlight gives 116/148 of maximal assimilation at 29°·5. Therefore, to give the whole maximal assimilation ($1\frac{1}{2}$ hours *ab initio*), there will be required 0·36 ($= \dfrac{148}{116} \times 0.28$) sunlight.

One might make an apparently more direct and absolute statement to the effect that *the photosynthetic energy in* 0·28 *sunlight is sufficient to reduce* 0·0116 *gramme* CO_2, but we shall see presently reason for regarding the statement which takes notice of the time-factor as a more critical and precise one.

Before going further into this matter, let us take a similar experiment with a leaf of *Helianthus*.

After several failures, in Experiment XVI we succeeded in getting all our data into one experiment.

The leaf was set up at 8 A.M., exposed to full intense sunlight *plus* diffuse light, and the assimilation value of 0·0290 was obtained at about 30° C. This we regard as obviously maximal for the temperature. To make certain of this, a second estimation was made with direct sunlight only, the diffuse light being cut out by the wooden tube. Again, in spite of the diminution of light, about the same assimilation, 0·0284, is obtained, and this point is proved. Then the diffuse light alone is employed (and, indeed, the sky had clouded up), giving a value of 0·0170, which is not nearly maximal for the temperature of 29°·5, but only about $\frac{3}{5}$ of the maximal amount. On the clouds clearing right away an estimation was made with 0·62 sunlight at 30° C., and this gave a value of 0·0224, large, but not maximal as was the case with cherry-laurel in this intensity of light. To conclude this satisfactory series, an estimation was again made in full sunlight, *plus* diffuse light, to get a maximal reading (one cloud came up at 2.6 P.M., and the current was shifted back to the preliminary tube till 2.29 P.M.). The value obtained was 0·0238, showing the usual effect of the time-factor, and falling off from the early value of 0·0290.

Connecting up (in fig. 6) the maximal values by a line, we find that at 1.15 the value would have been 0·0248. So at that hour 0·62 sunlight gave 224/248 of maximal assimilation at about 29°·5 (5 hours *ab initio*); therefore, for the whole maximal assimilation, 0·69 sunlight is required.

The absolute form of statement would be that 0·62 sunlight can reduce 0·0224 gramme CO_2.

Experiment XVI (August 8, 1904).—*Helianthus tuberosus* ; Weight, 1·30 grammes ; Area, 59·0 sq. cm. ; Current Rate, 800 c.c. ; CO_2 = 6·3 per cent. (average).

Exposure.	Time.	Illumination.	Temperature of bath.	Temperature of leaf.	CO_2 supplied.	CO_2 absorbed by leaf.	Real assimilation per hour per 50 cm².
Leaf exposed to full sunlight *plus* diffuse light	A.M. 8·5—9.5	Brilliant sun	24·8	29·6	Preliminary		
	9.5—9.35	,,	24·8	29·3—31·0	0·0469	0·0159	0·0290
Whole sunlight only ; wooden tube	9.35—10.3	,,	23·5	29·0	0·0509	0·0156	0·0284
	10.3—10.33	,,	23·5	29·2			
Diffuse light only ; shadow-board	10.33—11.7	Cloudy	—	29·0			
	11.7—11.30	Dull	28·5	29·5			
	11.30—noon	,,	28·5	29·5	—	0·0089	0·0170
Leaf exposed to 0·62 sunlight ; wooden tube with wire gauze	P.M. noon—1.6	Clouds ; brilliant sun after 12·55	27·6	30·0			
	1.6—1.36	Brilliant sun; no clouds	27·6	30·0	0·0514	0·0120	0·0224
Full sunlight *plus* diffuse light	1.36—1.55	Bright sun	—	29·0			
	1.55—2.48 (30 mins. sun)	,, (one big cloud)	—	29·5	0·0550	0·0130	0·0238
Darkened	4—6	Dark	19·0	19·0	—	Respiration 0·0007½	

Let us now compare the results with these two very different types of leaf:—

Cherry-laurel...   0·28 sunlight gives 0·0116.   ∴ full sun = 0·0414
Helianthus ......   0·62 sunlight gives 0·0224.   ∴ full sun = 0·0361

The sun with the cherry-laurel was $1\frac{1}{2}$ hours before noon, and with *Helianthus* was $1\frac{1}{4}$ hours after noon, so no correction is to be applied on that account.*

The larger value was obtained on August 16, and the smaller one on August 8, when the brightness of the sun at noon is about 3 per cent. greater, so that correction for the greater air mass traversed by the rays of the lower sun of the later date would tend to bring the numbers further apart by this amount.

Apart from any correction there is a fair agreement between these values as indicating that the full sun, about noon, about the middle of August, radiates enough light on to 50 sq. cm. of leaf surface, normally exposed, to reduce 0·04 gramme CO_2 per hour.   At the summer solstice the value should be about 6 per cent. larger.

There is, however, a biological correction, legitimately to be applied to the two values, which brings them much closer together.   This turns on the fact that the value for cherry-laurel was determined $1\frac{1}{2}$ hours after starting assimilation, while for *Helianthus* it was 5 hours after starting ; the " time-factors " are different.

There is evidence, to be considered in a separate paper, that the time-factor at high temperatures is not of the nature of a limiting factor, but involves a falling-off of the efficiency of the chloroplast machinery of such a nature that it takes, to put it crudely, continually more energy to reduce a given amount of CO_2.   The chloroplast will, at any time, require a fixed amount of light-energy, but will reduce less and less CO_2; also, with any less amount of energy, there will be a proportional decrease in the amount of CO_2 reduced.   If, then, at any one moment at the temperature of 29°·5 with cherry-laurel, 0·36 light gives maximal assimilation, then, according to this interpretation, it would give it also at any other moment.

So, also, with *Helianthus*, 0·69 light will always give just the maximal assimilation at this same temperature.

What, then, is the ratio of the maximal assimilation at about 29°·5 C. for these two leaves ?   Fig. 6 shows that, for those times at which there is

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* Crova has shown that after noon the more abundant water vapour renders the atmosphere less transparent to heat radiations than before noon, but there is no evidence that this holds for light.

evidence as to both, the value for *Helianthus* happens to be 1·95 times that for cherry-laurel. We should expect *Helianthus* to require 0·71 sun if cherry-laurel requires 0·36, and what it does require is 0·69 of sunlight 8 days nearer the summer solstice, when the sun is 3 per cent. brighter. This correction for the time-factor then brings the estimations into extraordinary close harmony, some of which is no doubt accidental, and may vanish with further experiments.

If the hypothetical initial values of the temperature maxima at 29°·5 C. really hold for any appreciable time, and the time-factor has the significance here attributed to it, then the full sunlight will have a higher absolute photosynthetic value than the observed value. For, *initially* :—

$$0\text{·}36 \text{ sun, on August 16, would give}\ldots\ldots\quad 0\text{·}0167$$
$$\text{and}\quad 0\text{·}69 \text{ sun, on August } 8, \text{ would give}\ldots\ldots\quad 0\text{·}0325$$

if these are the initial maxima for cherry-laurel and *Helianthus* respectively at this temperature.

On this basis—

$$\text{Full sun, on August 16} = 0\text{·}0464$$
$$\text{Full sun, on August } 8 = 0\text{·}0471$$

which values have about the right proportion for the brightness of the noon sun at these two dates.

The photosynthetic value of the full noontide sun at the summer solstice would then be about 0·050 gramme CO_2 per 50 sq. cm. of leaf surface normally exposed at this latitude.

These refinements of correction have no great significance till more estimations have been made, but somewhere between 0·05 and the uncorrected value of 0·04 the actual value will lie.

Section VI.—*The Specific Assimilational Characteristics of Diverse Leaves.*

This section will be devoted to some physiological considerations suggested by the differences in functional activity of the two types of leaf with which we have worked.

For one thing we find that the two leaves do not have the same assimilation-maxima at identical temperatures. This in itself does not greatly surprise, and one might expect that the " less active " leaf of cherry-laurel would perhaps reduce less CO_2 for the same amount of energy—that there would be different specific economic coefficients of chloroplast activity for the two leaves. In that case there would possibly be a constant ratio shown between their curves of assimilation-maxima. Inspection of fig. 2 shows that this is not so. The maxima are, at 18° C., in the ratio of 1 : 1·2, and at 29°·5 C. as

1 : 1·95.   We have, however, proved in the last section that at this higher temperature *Helianthus* requires twice as much light to reach its maximum as does cherry-laurel.

This suggests that the same amount of CO_2 is reduced in both plants by the same intensity of light.   At 18° C. *Helianthus* would then require only 1·2 times as much light as cherry-laurel for its maximal activity.   The limitations set upon the *activity* of leaves by various temperatures would then be secondary in nature, and be merely superposed upon a primary and uniform relation between energy absorbed and work done.

The only observations that militate against this uniform relation are those dealing with the decline of assimilatory activity with continued exposure to high temperatures.   These effects of the "time-factor" appear not to be such as a limiting factor would produce, but rather to indicate a smaller economic coefficient of activity.

This evidence must be postponed for the present, but we propose to give now experiments to prove that at temperatures not involving the time-factor, equal intensities of light produce the same amount of reduction of CO_2 even with very diversified types of leaf.

These experiments were carried out with artificial light (Keith high-pressure incandescent gas light) just in the same way as the experiments in "Assim. and Resp. III."

The leaf-chamber was contained in a water-bath at a uniform temperature of 25° C.   The source of light was removed to such a distance that it only caused an assimilation of about 0·0085 gramme CO_2 per hour per 50 sq. cm. leaf-area.   It was thus well below the assimilation-maximum for the temperature, which is, with cherry-laurel, 0·0114.   This, of course, is of fundamental importance, and ensures that the amount of assimilation will really be a measure of the light-intensity.

The light used has an arbitrary intensity depending on its distance from the bath; its intensity was not determined in any optical unit, but is expressed in terms of its reducing power for CO_2 with a cherry-laurel leaf.

We first compared a leaf of *Tropæolum* with one of cherry-laurel.   The experiments were as follows :—

Experiment XVII.—*Tropæolum* (October 8, 1904).   Weight of leaf, 1·25 grammes ; Area, 53·2 sq. cm.

Time.	CO_2 supplied.	CO_2 absorbed.
10.45—noon	Preliminary	
12—1	0·0283	0·0086
1—2	0·0289	0·0080
2—3	0·0295	0·0078

Mean apparent assimilation .... 0·0081
Respiration, 7.30—11.30, 0·0028 in four hours ... 0·0007
_____
Real assimilation per leaf .... 0·0088
  ,,   ,,   per 50 sq. cm. .... 0·0083

Experiment XVIII.—Cherry-laurel (October 10, 1904).   Weight of leaf, 1·90 grammes ; Area, 54·3 sq. cm.

Time.	CO_2 supplied.	CO_2 absorbed.
10.45—noon	Preliminary	
12—1	0·0334	0·0080
1—2	0·0344	0·0082
2—3	0·0348	0·0082

Mean apparent assimilation .... 0·0081
Respiration, 7.30—11.30, 0·0049 in four hours ... 0·0012
_____
Real assimilation per leaf.................... .... 0·0093
  ,,   ,,   per 50 sq. cm. .... 0·0085

Then, at another time, we compared the leaves of *Bomarea* and *Aponogeton* with cherry-laurel, using approximately the same position of the light.

Experiment XIX.—Cherry-laurel (December 7, 1904).   Weight of leaf, 2·15 grammes;   Area, 62 sq. cm.

Time.	CO_2 supplied.	CO_2 absorbed.
11.15—noon	Preliminary	
12—1	0·0378	0·0095
1—2	0·0393	0·0102
2—3	0·0384	0·0104
3—4	0·0371	0·0094

Mean apparent assimilation ....   0·0099
Respiration, 5.30—11.30, 0·0066 in six hours ...   0·0011

Real assimilation per leaf................. ....   0·0110
„   „   per 50 sq. cm. ....   0·0089

Experiment XX.—*Bomarea* (December 8, 1904.)   Weight of leaf, 1·40 grammes;   Area, 51·7 sq. cm.

Time.	CO_2 supplied.	CO_2 absorbed.
11.15—noon	Preliminary	
12—1	0·0360	0·0092
1—2	0·0336	0·0083
2—3	0·0352	0·0081
3—4	0·0352	0·0076

Mean apparent assimilation ....   0·0083
Respiration, 6—12 night, 0·0027 in six hours ...   0·0005

Real assimilation per leaf.............................   0·0088
„   „   per 50 sq. cm. ....   0·0085

Experiment XXI.—*Aponogeton* (December 10, 1904).   Weight of leaf, 1·60 grammes;   Area, 39·5 sq. cm.

Time.	CO_2 supplied.	CO_2 absorbed.
12.30—1.15......	Preliminary	
1.15—2.15......	0·0400	0·0072
2.15—3.15......	0·0410	0·0066
4.45—5.45......	0·0418	0·0066

Mean apparent assimilation ....   0·0068
Respiration, 7.20—11.20, 0·0015, in four hours...   0·0004

Real assimilation per leaf............. .. ..   0·0072
„   „   per 50 sq. cm. ....   0·0091

The leaf of *Aponogeton*, which normally floats on water, was here simply stood up with its cut stalk dipping in the water at the bottom of the chamber. The air in the chamber was quite damp, and the leaf showed no signs of wilting at the end of the experiment. *Bomarea* is a climbing monocotyledon with its morphologically upper leaf-surface downwards.

The four other leaves examined, then, agree with our standard within 5 per cent., and the diversity of type of these five seems to us to be wide enough to prove that *leaves in general have the same coefficient of economy in the photosynthetic process.*

There is, then, no difference in leaves in this direction, and it would appear from fig. 2 that even their temperature-maxima would be the same at very low temperatures. The fundamental existing specific differences would seem to lie in their different coefficients of acceleration of activity with increase of temperature. For a rise of 10°, the increase with cherry-laurel is 2·1 [0·0038 at 9° and 0·0080 at 19° C.], while with *Helianthus* it is certainly bigger, perhaps 2·5, but we have not exact data yet for giving the coefficient a precise value.

Perhaps this specific difference of the coefficient of temperature acceleration holds with growth and other metabolic processes, and a high coefficient might be a general characteristic of those plants which are recognised to be very "active" in vegetation.

The general views expressed in this paper involve the assumption that *with all intensities of light the amount of assimilation is proportional to the intensity of the light* unless some secondary or limiting factor is at work. Timiriazeff* has recently expressed the view that for plants (in general) there is a maximum of assimilation corresponding to half the intensity of direct sunlight, and that with higher intensities no further increase of assimilation takes place.

We feel convinced that this result is due to the neglect of some limiting factor, probably the temperature, the effect of which has been ignored by nearly every investigator of these questions. By selecting an appropriate temperature one can get a maximum of the kind described by Timiriazeff at any desired low fraction of sunlight for any given leaf.

There is certainly no *general* value for the fraction of sunlight utilised by leaves, either at a given temperature, or at the highest functional temperature, but, on the contrary, it is just on this point (being a consequence of the combined principles of uniform economic coefficient and varied

* Timiriazeff, 'Roy. Soc. Proc.,' vol. 72, p. 451, 1903.

temperature-acceleration coefficients) that leaves differ specifically one from another.

It follows that there is *no optimum* of light-intensity for assimilation, even for specific leaves, still less generally.

Section VII.—*The Limitation of Assimilation by the Natural Environment.*

The relation of the respective intensities of sunlight, diffuse sky-light, and total light become of interest in connection with our estimations, and with the general question of the available illumination for "sun plants" and "shade plants." The relation of these intensities has been calculated for a cloudless sky by Clausius.[*] The calculations are based on a summing up of the various orders of reflections of that part of the sunlight which is scattered in passing through the atmosphere.

Assuming the light that would reach a horizontal surface on the earth from a vertical sun to be unity, if the atmosphere were absolutely clear and did not scatter any of it, Clausius calculated that with the sun at an altitude of 60°, the direct sunlight would be 0·621 and the diffuse light 0·176, while at an altitude of 30°, the former would be 0·281 and the latter 0·138, and at an altitude of 10°, the former 0·033 and the latter 0·067.

Thus, as the sun sinks the ratio of the diffuse light to the sun-light increases, being about 1 to 2 at 30°.

Several observers have made direct observations on these points, using the darkening of photographic sensitised papers as a measure of light intensity. This only gives a measure of the more refrangible rays, and is generally spoken of as the "chemical intensity" of the radiation.

Brennand[†] made measurements in the cloudless sky of India and exposed his paper (1) at right angles to the sun's rays alone in a dark chamber; (2) in shadow of a stick to sky alone; and (3) to sun and sky together.

With the sun below the altitude of 13°,[‡] the whole diffuse light is more active than direct sunlight alone. Above 13° he found the following values as means of a large number of observations :—

Sun's altitude.	Sunlight.	Sky-light.	Total light.
13°	0·0377	0·0376	0·0782
30	0·1070	0·0628	0·1698
45	0·1429	0·0700	0·2128
60	0·1620	0·0727	0·2347
90§	0·1751	0·0743	0·2404

[*] Clausius, 'Poggendorff Annalen,' vol. 72, 1847.
[†] Brennand, 'Roy. Soc. Proc.,' vol. 49, 1891.
[‡] Roscoe found the altitude for equality to be 19°.
[§] The values for 90° were obtained by calculation.

Here we note that sky-light increases its ratio to sunlight as the altitude decreases, being just half at 45°.

For a *horizontal* surface on the earth Brennand calculates from the above data :—

Sun's altitude.	Sunlight.	Diffuse light.	Total light.
15°	0·012	0·051	0·063
45	0·069	0·083	0·152
60	0·140	0·089	0·229

These numbers show how large a part diffuse light plays in the total illumination when the sun is low.

Roscoe[*] has made a large number of measurements of "chemical intensity" of radiation by the photographic method worked out by Bunsen and himself in 1862. He finds that the "chemical action" (*i.e.*, that on sensitised silver paper) of the sun depends only on its altitude independently of the hour of day or the latitude.

The presence of clouds causes large departures from the values calculated or found for cloudless skies; the "clouds act as mighty reflectors of light" and "the presence of a thin film of cloud may enormously increase the *total* chemical intensity."

The rays that act on silver salts do not, however, play the chief part in assimilation. Objective measurements of the intensity of action of the less refrangible rays of natural light have not, so far, been carried out. Possibly, the activity of the living chloroplast may be yet used for this purpose.

Measurements of the intensity of total daylight on a horizontal plate have been made daily at noon for some years by L. Weber.[†] He measured the intensity of the red rays (about $\lambda = 630$) and the green rays (about $\lambda = 541$) of the total daylight, comparing them photometrically by eye with the same rays in a standard artificial light. He finds that the ratio of red to green varies in the daylight independently of its intensity.

The highest value observed in three years for the total daylight at noon was on July 5, viz., 154,300, and the minimum on December 12, viz., 655, the total mean of the three years being 36,185 metre candles.

The amount of the total daylight on any given day that is attributable to diffuse sky-light was arrived at by deducting the *calculated* brightness of the sun's direct light at noon on that day. In this way it is shown that on some days, with the suitable arrangement of clouds, even at noon the total light

* Roscoe, 'Phil. Trans.,' 1863, 1865, 1867, 1870; and 'Roy. Soc. Proc.,' vol. 15, 1866.

† L. Weber, 'Meteorol. Zeitschrift,' vol. 2, 1885; and 'Schriften Naturw. Vereins, Schleswig-Holstein,' vol. 10, 1895.

may be as much as three or four times that of the sun alone, and that too, in summer.

As regards red rays, the noon-total-daylight curve for the year agrees very closely with that calculated for red rays in clear sun alone, so that the clouds appear to reflect upon the earth just about as much red light as they stop out of the direct sunlight. This would tend to discount the influence of sunlight in a process such as assimilation.

As regards green constituent rays it is different, and the clouds in general reflect much more than they stop directly out of the sun's rays. A few observations made concurrently on the "chemical intensity" of the action of total daylight at noon on sensitised paper seemed to show that the actinic rays are proportional to the red, and about 25 times as intense (in ratio that is, to the relative abundance of these two kinds of rays in a normal candle).

The whole trend of these observations is to increase our *a priori* estimate of the assimilatory value of diffuse light as compared with direct sunlight.

This also has been the outcome of the measurements recorded in this paper. The highest assimilatory value of diffuse light recorded is 0·0192 gramme CO_2 in Experiment IX, and this is equal to all the assimilation that is possible at about 27° C. with *Helianthus*, or at 34° C. (31° initially) with cherry-laurel.

The intensity of the blue rays will not always serve as a measure of the intensity of the red rays, particularly so when the sun is low in the heavens. Abney[*] has measured the brightness of the various parts of the solar spectrum with different altitudes of the sun. The smaller the altitude, the longer is the path that the sun's rays travel through the atmosphere, and as the air is more absorbent for blue rays, so these tend to die out more and more as the sun sinks and the light becomes redder. We may quote the following data :—[†]

Sun's altitude............	90°·0	30°·0	14°·3	7°·3	about 0°
Atmospheric mass	1·0	2·0	4·0	8·0	32·0
Red, A, $\lambda = 0.76$	0·95	0·91	0·81	0·66	0·107
Orange, D, $\lambda = 0.59$ ...	0·87	0·75	0·57	0·32	0·001
Blue, F, $\lambda = 0.49$	0·74	0·54	0·30	0·09	0·000
Total sun brightness ...	0·84	0·70	0·50	0·21	0·002

In this connection it is interesting to recall how late in the evening assimilation can be detected. The rays active in photography die out rapidly towards sunset, but Experiments II, III, and IV show that the red rays

[*] Abney, 'Phil. Trans.,' 1887 and 1893.
[†] Hann, 'Lehrbuch der Meteorologie,' Leipzig, 1901, p. 13.

persist later and that assimilation actually overbalances respiration until sunset, and continues to cause a gain of material to the leaf up to that time.

From natural illumination in relation to assimilation-intensity we may turn now to the question of natural temperature in the open air.

The temperature of a leaf in the shade will equal the air-temperature within a degree or so, and the temperature may therefore well be so low that it would prevent the light producing its full effect, and the temperature would then in Nature, as in many of our experiments, be a limiting factor.

If we assume that a cherry-laurel leaf in the shade is just about the air-temperature, our curve of assimilition-maxima in fig. 2 shows us at once to what extent the assimilation would be limited by the temperature. Let us take the particular case of August 7, when the diffuse light was sufficiently bright to give an assimilation of 0·0192 in the shade. We construct the following table of the effect at different temperatures :—

Leaf-temperature.	Assimilation possible.	Percentage of available light utilised.
18° C.	0·0075	39
22	0·0097	50
28	0·0135	70

In direct sunshine in open air the case would generally be different, and the absorption of total radiation by the leaf would so raise its temperature as to make it capable of utilising a larger part of the rays specific to photosynthesis.

We may consider further cases from our work. The cherry-laurel leaf in brilliant sunshine in the open air reaches possibly a temperature of 9° to 13° C. above the mercury thermometer in the sun, say a temperature of 39° C. for a bright hot day ; this corresponds theoretically to an initial assimilation value of 0·0352 gramme CO_2 per 50 sq. cm. per hour, which is about three-quarters of 0·047 gramme CO_2, the calculated "initial" value for full intensity of August sunshine, and distinctly less than the possible value of full sunshine *plus* general diffuse light at the summer solstice.

For *Helianthus* the temperature-coefficient is larger and the temperature maxima run up very rapidly at high temperatures. We have as yet no data for this leaf above 30° C., but continuing the curve upwards freely the theoretical initial value of 0·05 might even be attained at 38° C. It seems clear that this leaf might for a short time utilise the whole of the specific radiation in full August insolation at some temperature above 35° C. The

temperature which a *Helianthus* leaf actually reaches in the sun in the open air is probably lower than with cherry-laurel by virtue of greater transpiration.

While then cherry-laurel in the sun would certainly have its assimilation limited by its temperature, *Helianthus* might not be thus limited when it attained a similar temperature. If, as seems probable, it only attains much lower temperatures, it also might be limited in sun alone, and certainly so when illuminated by direct insolation *plus* bright diffuse light.

Besides the illumination and the temperature there is a third factor which may function as a limiting factor. This is the partial pressure of CO_2 in the atmosphere surrounding the leaf. In all our experiments the air-current has been enriched with CO_2, so that only in one case, and that unintentionally, has the CO_2-supply been a limiting factor. How different is it in Nature!

All the considerations that we have adduced regarding the extreme values of assimilation with full intensity of illumination and the highest temperatures come to nought, at least, as far as their direct existential import, when we realise that nowhere in nature is there sufficient carbon-dioxide in the environment to permit of anything approaching such intensity of assimilation.

We may take it that the CO_2 in the atmosphere rarely exceeds three parts in 10,000 (except indeed in London fogs), and we have to enquire to what maximum of assimilation this will limit a leaf in the open air. We have made no experiments on this point ourselves, but the experiments of Sachs and of Horace Brown furnish us with data.

Horace Brown[*] has shown that a surface of caustic alkali exposed in the open air containing 3 parts in 10,000 of CO_2, absorbs per hour and per square metre 1200 c.c. of this gas when the air is still and up to 1500 c.c. if the air is agitated by wind.

Brown and Morris[†] have also determined the amount of CO_2 taken in by a leaf of *Helianthus* in the open air, by measuring the increase of dry weight after the method of Sachs.

On a bright warm day a cut leaf gained 1 gramme dry weight per hour per square metre and on a dull day a cut leaf gained 0·985 gramme, this gain is to be treated as if it were all carbohydrate of the cane-sugar type. Expressing the results in grammes CO_2 per 50 sq. cm. of area per hour, we get the following absorptions :—

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[*] Address to the Chemical Section, British Association, 1899.
[†] 'Journal of the Chemical Society,' 1893, p. 604.

$$\begin{array}{ll}
\text{Caustic alkali, still air} \ldots\ldots\ldots\ldots & 0\cdot 0117 \\
\text{,,}\qquad\qquad \text{wind} \ldots\ldots\ldots\ldots\ldots & 0\cdot 0148 \\
\textit{Helianthus} \text{ leaf, bright day} \ldots\ldots\ldots & 0\cdot 0079* \\
\text{,,}\qquad\qquad \text{dull day} \ldots\ldots\ldots\ldots & 0\cdot 0077
\end{array}$$

Sachs arrived at a much higher number for *Helianthus*, viz., 0·150, but this was not directly observed; it was arrived at by employing a leaf attached to its plant and making a large allowance for translocation, based on another experiment. Sachs' number probably is much too high.

From the fact that the same number was arrived at by Brown and Morris on two days, one brightly lighted and the other dull, we may conclude that the intake of CO_2 was really limited by the diffusion possibilities and not by the light or temperature.

This view is supported by the experiments in the present paper, which show that this *intake* of CO_2 can be much surpassed with moderate illumination when the CO_2-supply is not a limiting factor. Thus with an adequate pressure of CO_2 we have recorded:—

$$\begin{array}{llll}
\text{Experiment XVI.} & \textit{Helianthus,} \text{ sunlight only} \ldots\ldots\ldots & = 0\cdot 0264\dagger \\
\text{,,}\qquad \text{XVI.} & \text{,,}\qquad \text{diffuse light only} \ldots & = 0\cdot 0151 \\
\text{,,}\qquad \text{XI.} & \text{,,}\qquad \text{faint sun} \ldots\ldots\ldots & = 0\cdot 0254 \\
\text{,,}\qquad \text{IX.} & \text{,,}\qquad \text{diffuse light only} \ldots & = 0\cdot 0192
\end{array}$$

It is probable then that a leaf of *Helianthus* is in Nature limited to an absorption of 0·0077 gramme CO_2 per hour per 50 sq. cm. The value may be higher even up to the 0·0150 of Sachs, but it does not seem likely that the leaf should be as efficient as an equal area of caustic alkali, even though this particular leaf has two absorbing surfaces. The evidence, on the whole, is not in favour of the view that leaves with stomata on both surfaces are much more efficient absorbers than those with stomata on one surface only. There are probably few leaves more active in assimilation than those of *Helianthus*, *i.e.*, few offering less mechanical hindrance to the ingress of CO_2, and if the lower value of 0·0077 is too low for this plant, it may be the limit for a number of other plants.‡

We will endeavour then to picture the state of things that holds with a leaf limited to this intake by the low pressure of CO_2 around it.

In setting out to compare the energy available for photosynthesis with the

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* A leaf of Catalpa (conditions of experiment not stated) gave also 0·0078, *cf.* Horace Brown, 1899, *loc. cit.*

† These numbers are the *apparent* assimilation, *i.e.*, the real assimilation less the respiration.

‡ See, however, Note C, p. 459.

work actually done under various environments, the fact must not be lost sight of that the leaf-cells are *respiring* in the light, and that the CO_2 that they produce has continually to be reduced by the radiant light-energy before so low a partial pressure of CO_2 is arrived at that further supplies may diffuse in from the atmosphere. The amount produced in respiration will vary with the temperature of the cells and may, at about 30° C., be equal to half the possible inflow from without.

The following table represents the waste of photosynthetic energy that may be considered to go on when the natural supply of CO_2 limits the intake to 0·0077, with various illumination and temperature.

The table avoids extreme intensities of illumination and deals with two that we have actually observed. The assimilation-maxima given in the third column are all observed values except the last, which is only an approximation. The energy is throughout expressed in terms of the work it can do in photosynthetic reduction, *i.e.*, in grammes CO_2 per hour per 50 sq. cm. leaf-area :—

Leaf.	Hypothetical temperature of leaf cells.	Assimilation-maximum.	CO_2 of respiration.	+	Intake of CO_2 from atmosphere.	=	Actual assimilation.	Aug. 8, 1904, noon.	
								In sun, 0 ·0530.§	In shade, 0 ·0170.
								Surplus energy.	Surplus energy.
	° C.								
Cherry-laurel	10	0 ·0042	0 ·0005	+	0 ·0037	=	0 ·0042	0 ·0498	0 ·0128
Helianthus ...	19	0 ·0098	0 ·0008	+	0 ·0077	=	0 ·0085	0 ·0445	0 ·0085
„ ...	29	0 ·0285*	0 ·0020	+	0 ·0077	=	0 ·0097	0 ·0443	0 ·0073
Cherry-laurel	37 ·5	0 ·0238†	0 ·0044	+	0 ·0077	=	0 ·0121	0 ·0409	0 ·0049
Helianthus ...	35	0 ·0400‡	0 ·0032	+	0 ·0077	=	0 ·0109	0 ·0421	0 ·0061

The last two columns show how large is the waste of photosynthetic energy with the limited intake of CO_2 that our atmosphere provides for.

It will be observed that raising the CO_2-content of the atmosphere from three up to six parts in 10,000 will, as Horace Brown has shown, double the intake, and this will do away with all waste of energy in the last four cases in the shade. To prevent this waste in the insolated leaf an increase of six fold,

* Observed $1\frac{1}{4}$ hours *ab initio*.

†   „   2   „   „

‡ Approximately estimated.

§ This represents the energy available for photosynthesis in Experiment XVI ; in that case (reading 4) 0·62 sun gave 0·0224 ∴ whole sun alone may be taken at 0·0360. The diffuse light (reading 3) was 0·0170 ; for a leaf freely insolated these two must be added together.

to about 18 parts in 10,000, would appear to be indicated.   As a matter of fact, if this were done the temperature would then become the limiting factor and each leaf would stop at the values given in column 3.   The waste would then be the difference between 0·0530 and the values in this column.

The leaf at 10° C. is, however, already limited by temperature, and cannot, therefore, avail itself of even half the CO_2 that might diffuse into it.

At hours remote from noon the solar radiation falling on a leaf will be much less intense, and the average for all the daylight hours of a year will be very much below 0·0530.

This consideration is of interest in relation to the theory that the reduction of carbon-dioxide by plants in the carboniferous epoch must have been much more energetic than at the present time to account for the deposition of such enormous masses of carbonaceous matter in the earth.

If the illumination was the same as at the present time, there would hardly have been enough energy for more than threefold intensity of total CO_2-reduction, however rich the atmosphere might have been in this gas.

The general lesson to be learned from these limitations of assimilation in nature would seem to be that the biological advantage which plants gain when dwelling in the brightest habitats, is not increased assimilation, but probably increased warmth.   This may be the explanation of the fact noted by Wiesner in his studies on "Lichtgenuss," that shade plants are abundant in the tropics, but gradually fail in northern latitudes, and are absent in arctic vegetation.

VIII.—*Conclusions.*

There are three conspicuous factors which control the amount of assimilation of carbon dioxide that a leaf can perform: (1) the intensity of the illumination, (2) the temperature of the leaf, and (3) the pressure of the CO_2 in the surrounding air.   If the illumination is feeble, though the other factors are favourable, then the amount of photosynthesis will be kept down and light will be a "limiting factor" to the process.   So similarly with the CO_2-supply, and also, as has been shown in the previous paper of this series, with the temperature.   For each temperature there is a definite amount of assimilation that a leaf can perform and no more.   For a given plant these amounts are very constant; at high temperatures the high rate of assimilation cannot be maintained for long, and a "time factor" comes in to complicate the relation.

The present work is an attempt to interpret the quantitative variations of carbon-dioxide assimilation, under natural or semi-natural conditions, in terms of these three chief factors.

When an increase of assimilation follows an increase in the sun's radiation

incident on a leaf, it requires special investigation to determine whether the effect is actually due to the increase of light or to the increase of temperature.

Single leaves of cherry-laurel or *Helianthus* were enclosed in a glass chamber sunk in a glass water-bath, of which the temperature could be controlled, and hourly or half-hourly estimations made of their assimilation under all varieties of natural illumination. The exact temperature of the leaf was determined thermo-electrically all through the experiments, and the illumination was either the natural diurnal sequence in the open air or selected illumination, *e.g.*, diffuse light alone, full sunshine alone, or definite fractions of sunshine. The current of air through the leaf chamber was enriched with CO_2, so that inadequate supply of this gas might never be a limiting factor.

To test whether an observed assimilation-value is limited by light or by temperature, it suffices to change the intensity of each factor separately. Thus, in the case that temperature is limiting, circulation of hotter water through the bath sends up the assimilation without any increase of illumination, while, if the temperature is carefully kept constant, the illumination can be increased to any extent without causing a rise of assimilation. Assimilation in shade and in sunshine was analysed in this way.

With a leaf exposed to diffuse daylight only, the amount of assimilation is a measure of the light if the temperature is kept high, and then the assimilation will fall all through the afternoon with the waning light. If the temperature is low, then assimilation is thus limited, and remains uniform all through the varying light. Real assimilation persists until sunset. The diffuse light may have a very high photosynthetic intensity when the sky is covered with white reflecting cumuli or with a thin haze.

With a leaf kept exposed normally to the sun throughout the day a very rapid rise of assimilation sets in at sunrise, but the amount of assimilation is generally limited by the temperature, since the illuminating effect of the sun exceeds its heating effect, especially when the leaf is included in a bath of circulating water.

To apply to assimilation in free air the data obtained with a leaf in a water-bath, it is necessary to know the actual internal temperatures that leaves attain in sun and shade in the open air. Thermo-electric measurements with leaves of cherry-laurel, exposed normally to brilliant insolation, showed that the internal temperature may rise more than 10° above that registered by a bright mercury thermometer in the sun: a leaf exposed in a closed glass vessel may be heated a further 10°.

At natural temperatures neither *Helianthus* nor cherry-laurel is capable

of utilising for assimilation the whole of the appropriate radiation in full sunlight, so experiments were made to determine what fraction of this is used at a given temperature. For cherry-laurel it was found that 0·28 sun, near noon, near the middle of August, can reduce 0·0116 gramme CO_2 per hour per 50 sq. cm. of leaf area. With *Helianthus*, 0·62 sunlight, at about the same time, reduced 0·0224 gramme. These indicate for full sunlight the photosynthetic values of 0·0414 and 0·0361 on the two occasions. Making a correction for the time factor, the values come out higher and still closer together.

The highest assimilation actually measured (Experiment XVI) was 0·0290 gramme CO_2 per 50 sq. cm. leaf area per hour for *Helianthus* at 29°·5 C. This is about 2900 c.c. CO_2 per square metre per hour.

The nature of the specific assimilational characteristics of different types of leaf was investigated, and it is shown that:—

1. Equal intensities of light, incident upon equal areas of different leaves, produce, when light is the limiting factor, equal *amounts* of assimilation. This is proved to be true within 5 per cent. for such diverse leaves as cherry-laurel, *Helianthus*, *Tropæolum*, *Bomarea*, *Aponogeton*.

2. All leaves have the same economic coefficient of photosynthesis, using the term in the narrow sense to refer only to those radiations specific to this process.

3. At low temperatures different leaves, such as *Helianthus* and cherry-laurel, have similar assimilation-maxima, but at high temperatures the maxima diverge. At 29°·5 C. *Helianthus* can assimilate twice as much CO_2 as cherry-laurel.

4. This is harmonised with the first law by showing that *Helianthus* requires just twice as much light to attain this double assimilation.

5. The essential difference between these two leaves lies in their having different coefficients of acceleration of their assimilation-activity with increase of temperature.

6. From this it results that the two leaves utilise different fractions of sunlight at any temperature : this fraction is to be found for any temperature by dividing the assimilation-maximum of the particular leaf at that temperature by the photosynthetic value of the sunlight.

7. There is no optimum intensity of light for assimilation.

In Nature, the high values of assimilation that are obtained experimentally cannot take place, because assimilation is limited by the small pressure of CO_2 in the atmosphere.

There is thus a general waste or diversion into other channels of the photosynthetic energy in sunlight and diffuse light.

A table is constructed, showing the amount of energy unutilised at various temperatures by different leaves, with such noontide illumination in sun and in shade as actually prevailed on a definite day.

Were the CO_2 in the atmosphere augmented moderately, then this would cease to be the limiting factor in the shade generally, and also in feeble sunlight. Temperature, unless unnaturally high, would then limit assimilation in Nature, and still prevent bright insolation producing its full effect.

[*Notes added July* 25, 1905. While this paper has been in the press, there has been published in this Journal an extensive paper on a cognate subject by Dr. Horace Brown and Mr. Escombe, entitled "The Physiological Processes of Green Leaves, with Special Reference to the Interchange of Energy between the Leaf and its surroundings" ('Roy. Soc. Proc.,' vol. B 76, 1905, pp. 29 to 111). The following notes are now added to indicate as briefly as possible the points of contact between that paper and our own.

As a point of general significance it must be noted that the expression "*amount* of assimilation" has not the same meaning in the two papers. We use the unqualified words to mean the total photosynthetic work done in any time, part of the CO_2 for this being, of course, drawn from the external air and part from the concurrent respiratory activity of the leaf. Brown and Escombe intentionally leave respiration entirely out of account, and the unqualified word "assimilation" with them refers only to the intake of CO_2 from without.

A (see p. 412). Brown and Escombe have published detailed balance sheets (pp. 100 to 111) of the "Thermal Interchange" between leaves and their surroundings under various conditions of natural illumination. One interesting feature of these tables is the estimation of the internal temperature of the leaf. The degree of accuracy of this estimation is dependent upon the degree of accuracy of the six following determinations : (1) the coefficient of absorption of radiation by the leaf ; (2) the specific heat of the leaf ; (3) the energy being expended in transpiration ; (4) the energy being expended in photosynthesis ; (5) the thermal emissivity of the leaf ; and (6) the effect upon this function of the particular velocity of movement of the surrounding air at the time. The temperatures arrived at by these truly admirable calculations are, however, in no case checked by actual determinations. The temperatures given in these tables for leaves in the sun in the open air are never more than 2° C. above the shade temperature of the air, while our few direct measurements with cherry-laurel leaves, brilliantly insolated, indicated 7° to 16° C. above the thermometer in the shade. Our method is not unexceptionable, but it does not seem probable that this divergence is to be wholly accounted for by the combined effects of faults of method, exceptional insolation, and thickness of leaf used. (Brown and Escombe employed only types of leaf which were thin.)

B (see p. 435). Our *a priori* criticism of the method of fractioning light by the use of "rotating sectors" has not the cogency given to it in the text. Consideration of a number of experiments, in which this method was employed by Brown and Escombe, allows one to see that the leaf behaves in assimilation as the eye does in vision, and that halving the light *in time* has, with all strengths of illumination, the same effect as halving it in intensity. The interest of the matter therefore shifts to the determination of the induction period and to finding at what slowness of rotation of the sectors the leaf begins to distinguish between the two methods of reduction of illumination.

C (see p. 454). Brown and Escombe have made special inquiry into the trustworthiness of Sachs' "increase of dry weight method" of estimating assimilation, and their verdict is very unfavourable.

The value of 0·0077 gramme that we have adopted for assimilation in the open air when the CO_2-pressure is the limiting factor, was obtained by Brown and Morris by this method, and is therefore subject to suspicion and is probably too high.

The new data for arriving at this most important value, brought forward by Brown and Escombe, and based on measuring the intake of CO_2 by a leaf in a glass chamber in a rapid current of ordinary air, show a very wide range of variation even for the leaves of a single species (0·0016 to 0·0047 gramme per 50 sq. cm. for *Polygonum Weyrichii*). Primarily, the degree to which the stomata are open and, secondarily, the magnitude of the concurrent respiratory production of CO_2, would seem to be the important factors in disturbing the inflow of CO_2 from without.

The highest value thus arrived at is 0·0047 for a detached leaf, and as attached leaves with stomata less widely open give smaller values, the number adopted by us may be much too high. This would increase the waste of photosynthetic radiation in Nature, but the information at present available is not sufficient to allow us to readjust the table on p. 455].

Note on the Mechanics of the Ascent of Sap in Trees.

By Professor J. LARMOR, Sec. R.S.

The following remarks, relating to one of the most powerful and universal of the mechanical operations of organic nature, are based mainly on the numerous experimental results reported in Dr. A. J. Ewart's recent memoir.* Their chief object is to assert the view that we are not compelled to suppose the sap, in the column of vessels through which it rises, to be subject to the great actual pressure, amounting in high trees to many atmospheres, that is sometimes postulated. It is hardly necessary to remark that the problem of the rise of sap is one of mechanics, in so far as concerns the mode of the flow and the propelling power.

Contrary to the view above referred to, it seems not unreasonable to consider that the weight of the sap in each vessel is sustained in the main by the walls and base of that vessel, instead of being transmitted through its osmotically porous base to the vessels beneath it, and thus accumulated as hydrostatic pressure.

We could in fact imagine, diagrammatically (as happens in ordinary osmotic arrangements) a vertical column of vessels, each provided, say, with a short vertical side-tube communicating with the open air, in which the pressure is adjusted from moment to moment, and yet such that the sap slowly travels by transpiration from each vessel to the one next above,

* 'Roy. Soc. Proc.,' vol. 74, p. 554 ; 'Phil. Trans.,' B, vol. 198, p. 41.